Endogenous programs and flexibility in bird migration

Akesson, Susanne; Helm, Barbara

Published in:
Frontiers in Ecology and Evolution

Publication date:
2020

Endogenous programs and flexibility in bird migration

Susanne Åkesson, Department of Biology, Center for Animal Movement Research, Lund University, Ecology Building, SE-223 62 Lund, Sweden, susanne.akesson@biol.lu.se
Barbara Helm, GELIFES - Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands; b.helm@rug.nl

Abstract

Endogenous programs that regulate annual cycles have been shown for many taxa, including protists, arthropods, fish, mammals and birds. In migration biology, these programs are best known in songbirds. The majority of songbirds rely on a genetic program inherited from their parents that will guide them during their first solo-migration. The phenotypic components of the program are crucial for their individual fitness and survival, and include time components, direction, and distance. This program is constructed to both guide behavior and to regulate flexible responses to the environment at different stages of the annual cycle. The migration program is driven by a circannual rhythm, allowing for, and resetting, carry-over effects. With experience, the migration decisions of individual migrants may be based on information learnt on breeding sites, wintering sites, and *en route*. At the population level, substantial variation in route choice and timing of migration may be explained by inherited variation of program components, by interactions with environmental and social factors, and by individual learning. In this review we will explore the components of endogenous migration programs and discuss in what ways they can lead to flexibility and variation in migration behavior.

1. Introduction: migrations over time and space

Migrations, which we here define as regular periodic movements, have been linked to fluctuations of relevant environmental factors, such as nutrients (Newton 2008; Häfker et al. 2017), breeding site or mate availability (Barlow et al. 1986; Hodgson and Quinn 2002; Friesen 2015), predation risk (Häfker et al. 2017; McKinnon et al. 2010), infection probability (O'Connor et al. 2018), and abiotic survival threats (e.g. severe weather or UV radiation; Hut and Beersma 2011; Reid et al. 2018). Such environmental fluctuations, and the associated periodic movements of organisms, usually recur on time scales defined by geophysical cycles: annual cycles caused by Earth's orbit around the sun, diel cycles caused by Earth's rotation around its axis, lunar cycles caused by the orbit of Moon around Earth, and tidal cycles caused by the combined movements of Earth and Moon (DeCoursey 2004; Fig. 1A). Their common, planetary basis makes these cycles predictable, even if their downstream environmental consequences (e.g., temperature or food availability) may be more variable. The principle predictability of environmental cycles has provided the substrate for organisms to evolve time-keeping mechanisms that are fitted to their life-styles and specific environments.

Organisms use biological time-keeping to predict upcoming changes, to prepare for them, and to spatially relocate in anticipation (Helm et al. 2017; Åkesson et al. 2017). In a nutshell, these mechanisms integrate internally generated (i.e. endogenous) rhythms and responses to environmental cues into timing programs. In migratory organisms, spatial features, for example direction of travel or magnetic field cues, are often included, so that even naive individuals can perform effective migrations (Kramer 1957; Åkesson et al. 2017; Reppert and De Roode 2018).

These intriguing spatio-temporal programs have been extensively studied from a full-cycle perspective in migratory organisms on all four predictable time-scales introduced above (Fig. 1A; annual, diel, lunar and tidal; e.g., Barlow et al. 1986; Gwinner 1996a,b; Åkesson et al. 2017; Haefker et al. 2017). Central questions in this research field are concerned with inheritance of migration programs, their integration of environmental cues, and their physiological and genetic mechanisms (van Noordwijk et al. 2006; Åkesson et al. 2017; Merlin and Liedvogel 2019). Here, we review key insights, and apply them to address sources of variation in spatiotemporal migratory traits within and among individuals, as well as among populations. Our

review is aimed at explaining how endogenous programs can generate, or counteract, variation in migration. Among the countless contributions to the field, we highlight those that in our view are most suitable to achieving this aim, rather than attempting to give a balanced or exhaustive record of this vast research field.

The review actively contributes to a collection of articles that constitute the *Frontiers* research topic *Flexibility in the Migration Strategies of Animals* (Senner et al. 2019). Coherently with this *Frontiers* research topic, we will focus on annual time scales, choosing birds as study subjects, but the principle considerations also hold for other time scales and other periodically migrating organisms. We also streamline the use of terminology in our article as laid out for the entire *Frontiers* research topic. To facilitate cross-fertilization of ideas, we will first clarify the terminology and conceptual background of migration programs, which are not widely known among field-based researchers. We will then explain in greater detail how migration programs work, how they interact with environmental information, and how they regulate aspects of variation. Thereafter we will discuss additional variation and its possible interpretation. We address these points from theoretical perspectives and illustrate them by selected examples. Due to both our own geographic location and geographic differences in research focus on timing programs, our article is greatly biased towards the northern hemisphere, with emphasis on European data, although we strove to give global examples.

2. Terminology and concepts

Flexibility, plasticity, variation: The central topic of this *Frontiers* research topic is *flexibility*, defined on an individual level as variation in traits that can be reversed in response to an individual's environment throughout their lives. Such trait reversals can for example be based on experience, can occur in response to inter-annual differences in environmental conditions, or can be a generic part of the annual cycle (i.e. life-cycle staging, *sensu* Piersma and Drent 2002). Variation through flexibility is distinguished from polyphenisms (*sensu* Piersma and Drent 2002), where individuals differ from each other irreversibly because of genetic differences. It is also distinguished from developmental *plasticity*, which denotes variation in traits that is irreversibly determined during ontogeny (*sensu* Piersma and Drent 2002). We here

adopt this terminology for coherence across the *Frontiers* research topic, diverging from our use elsewhere (Helm et al. 2017).

Additionally, we will introduce a distinction between two types of flexibility. Because migration programs by definition regulate responses to the environment, we consider a substantial proportion of flexibility to be *programmed* (i.e., resulting from inherited reaction norms; van Noordwijk et al. 2006; Visser et al. 2010; Helm et al. 2017). A remaining part of *residual* flexibility is not readily explained by our current knowledge of migration programs. On a population level, we will refer to differences in migration as variation because their mechanistic basis is not clear. Differences in individual traits, such as timing or route choice, and in strategies, such as partial or differential migration, could be based on genetic differences, developmental plasticity, or individual flexibility.

Ontogenetic perspective: Additional emphasis in this *Frontiers* research topic is on ontogenetic variation in migration. From a perspective of migration programs, the main distinction is between an individual's first journey and its subsequent migrations. During their first migrations, juveniles are naive and depend on their programs, on social guidance, or on trial and error. In subsequent years, birds will have additional experience (Perdeck 1958), which may override the initially expressed migration program. A further distinction will be made between open-ended learners and those that adhere to their first experience for their future migrations (Gill et al. 2014).

Carry-over effects: A full annual-cycle perspective is at the heart of research on migration programs (Gwinner 1996b; Briedis et al. 2016), and hence, carry-over effects have long been studied within this field. In adherence to the lay-out for the present *Frontiers* research topic, we adopt a broad definition of carry-over effects to include all instances when previous history explains current performance, as long as they are functionally important and separated in time (O'Connor et al. 2014). Hence, learning and developmental adjustments mostly fall also under this definition.

From a perspective of timing programs, a distinction is made between carry-over effects within an annual cycle, and those between cycles. In many species, the timing program allows for high variation during some phases of the annual cycle, whereas during others individuals resynchronize to environmental cues and reset their annual

timing (e.g., Helm et al. 2005; Conklin et al. 2013; Karagicheva et al. 2016; Briedis et al. 2018; Gow et al. 2019). Thus, we consider carry-over effects *within* an annual cycle as flexibility that can be regulated by the migration program. In contrast, we view carry-over effects *between* annual cycles as modifications of the migration program, for example due to experience or to poor state. In either case, we view carry-over effects as an outcome of trade-offs, or, alternatively phrased, of different optimization criteria (Alerstam and Lindström 1990). Animals may compromise optimal timing for other benefits, such as improved state or additional broods, but may pay costs for suboptimal timing at subsequent annual-cycle stages (see also Senner et al. 2015). Alternatively, they can adhere to timing, at potential costs to state (i.e., departing in poor condition) or to reproduction (e.g., skipping a breeding opportunity to depart in time).

Migratoriness: Species differ greatly in the level of variation of their migrations (Newton 2008). Generally, spatio-temporal precision and consistency increase with migration distance, with proportion of population members migrating, and with the rigidity of its regulation (Newton 2008; Tryjanowski et al. 2005). This trend can be captured in the term migratoriness. Migration programs are most useful if birds move between sites that are spatially too distinct to assess environmental conditions of goal areas, and if conditions at the goal areas are sufficiently predictable to facilitate evolution of migration programs. If these conditions are met, birds tend to score high on migratoriness. An example for clear differences in migratory precision of related species with similar ecology are waders on Iceland, where relatively short-distance migrants (e.g., Black-tailed Godwits, *Limosa limosa islandica*) have substantially advanced arrival time over the last decades (Gill et al. 2014), whereas a long-distance migrant (Whimbrel, *Numenius phaeopus islandicus*) has not (Carneiro et al. 2019).

3. Migration programs for time and space

As new data from avian migrations flood in during this golden age of bio-logging (McKinnon and Love 2018), efforts to distill patterns have invigorated interest in migration programs. Consistent timing is perhaps the most commonly emerging pattern (Altshuler et al. 2013; McKinnon and Love 2018; Briedis et al. 2018; Carneiro

et al. 2019; Gow et al. 2019). Routes are often more variable (Stanley et al. 2012, Vardanis et al. 2016), although in some studies they were more consistent than timing (Vardanis et al. 2011; Sugasawa and Higuchi 2019). When timing is consistent within individuals, there may be large variation within and between populations, for example in departure date of sympatrically overwintering individuals (e.g. Conklin et al. 2010, 2013; Briedis et al. 2016; cf. Gow et al. 2019).

Much of the new evidence fits well with our current understanding of migration programs. Researchers had long postulated the existence of innate programs to explain why migratory birds do not simply stay at the wintering grounds, and how they return for breeding at the right time of year. Support for innate programs first came from observations by bird fanciers. When wild conspecifics would migrate, caged birds, provided with ample food and shelter, also performed migration-like behaviors (Birkhead 2008) and directional movements (e.g. Kramer 1957). This behavior is called migratory restlessness, or Zugunruhe. It is most readily observed in nocturnally migrating species which show bouts of migratory restlessness at night, but similar arguments have also been made for some diurnally migrating species (e.g. Bojarinova and Babushkina 2015). It is important to note that the restless hopping and flying in cages does not directly represent migration, but rather a captive expression of motivation to migrate (Helm 2006; Van Doren et al. 2016; Bäckman et al. 2017). However, this frustrated movement state (John Rappole, pers. comm.) often captures important aspects of migration and has been key to our understanding of bird migration. Migratory restlessness has been reported for many northern hemisphere-breeding migrants that breed in Europe, America and Asia. Species included mainly passerines and some other taxa, for example quail (e.g. Helms 1963; King and Farner 1963; Gwinner 1996ab; Budki et al. 2009; Bertin et al. 2007; Eikenaar et al. 2014; Watts et al. 2016). For tropical and southern hemisphere breeders, only a few Zugunruhe records exist, including intra-tropically migrating yellow–green vireos, *Vireo flavoviridis*; Styrsky et al. 2004) in the Americas, for stonechats in Africa (*Saxicola torquata axillaris*, Helm & Gwinner 2006, which however are locally resident), and for Australian silvereyes (*Zosterops lateralis*; Chan 1995).

Although migratory restlessness is not always easy to interpret, its regulation through robustly innate programs was confirmed in migratory birds that were kept under

constant conditions of daylength, temperature and food (Gwinner 1986; 1996b; Holberton and Able 1992). Over many years Zugunruhe alternated with moult and with reactivation of the reproductive system approximately annually (hence, called circannual). Thereby, it became clear that life-cycle stages including migratory behaviors were driven by an endogenous (i.e., self-generated) circannual rhythm. Furthermore, when tested for their directional preference, birds shifted the orientation of their Zugunruhe activities as appropriate for the corresponding leg of migration (Gwinner and Wiltschko 1980). A host of additional physiological changes that enhance migration also occurred (e.g., hyperphagia, fuel deposition; King and Farner 1963, Gwinner 1996a, Newton 2008). Migratory activity within this endogenous migration program is encoded in individual birds in relation to migration distance, with short-distance migrants generally expressing shorter periods of migratory restlessness than long-distance migrants (e.g. Berthold 1973, Berthold and Querner 1981, Maggini and Bairlein 2010, Bulte and Bairlein 2013). Because the endogenous migration program also encodes migration direction, it can lead migratory naïve individuals along routes to population-specific wintering areas (e.g. Helbig 1991).

3.1. Time

Annual timing: Under constant conditions, without any changes in the captive environment, circannual cycles recur, but their period lengths are ca. 9-15 months, so that life-cycle stages usually drift to occur at earlier or later dates over progressive years (Gwinner 1996b; Karagicheva et al. 2016). In nature, conversely, annual cycles do not drift, and life-cycle stages recur annually, usually at similar dates. Hence, it became clear that the circannual clock functioned in interaction with environmental cues that synchronize and modify its timing. Therefore, a spate of experimental studies investigated the synchronizing effects of environmental factors on migration programs across the annual cycle (Gwinner 1996b; Helm et al. 2009).

Among the synchronizing cues,photoperiod, the annually changing light fraction of the 24 h day (Fig. 1B), has the strongest effects, and can both, advance or delay the annual cycle. For example, in multi-brooded species, chicks hatch at widely different times of year. The correspondingly different daylengths experienced in early life can then synchronize chicks from consecutive broods. The contribution of the timing program to synchronizing these birds is illustrated by data from captive stonechats

(*Saxicola spec.*) from three regions (Europe, East Africa, Kazakhstan) that bred under naturally changing daylengths (Helm et al. 2005; Fig. 2). Chicks that grew up under shorter photoperiods, simulating late hatching at the end of summer, compensated by accelerated postjuvenile development in population-specific ways. Late-hatched of all populations largely caught up with earlier-born conspecifics by advancing autumn Zugunruhe by 0.9 days per day of later hatching. By this genetically programmed compensation mechanism, which was confirmed by field observations from wild conspecifics, stonechats achieved a high level of within-population synchrony (Helm et al. 2005) that counteracted carry-over effects of late hatching. Similar advancement of Zugunruhe for later-hatched chicks was also observed in birds breeding at low latitudes, for example in yellow–green vireos (Styrsky et al. 2004).

Synchronization within populations that counteracts carry-over effects also occurs at the end of overwintering when migrants initiate spring migration (Conklin et al. 2013; Senner et al. 2014; Briedis et al. 2018). For example, recent work on socially migrating tree swallows (*Tachycineta bicolor*) suggests that differential timing of migration may continue as a domino-effect set by breeding latitude until resynchronization in the winter quarters (Gow et al. 2019). Such resetting effects can be so strong that the non-breeding period has been described as buffering the build-up of carry-over effects (Senner et al. 2014; Briedis et al. 2018). However, for low-latitude wintering grounds, where photoperiod undergoes little change, it is still unclear how such synchronization is achieved, although effective cues have been described for breeding in equatorial birds (e.g. Goymann et al. 2012; Shaw 2017). A key property of timing programs is that the responses to environmental factors, which they encode, are specific to stage (phase) of the annual cycle (Fig. 3). It is intuitively sensible that a migratory bird would respond to a long, warm day differently on the breeding grounds than at its winter quarters. The same environmental cues can thereby cause either advances, delays, or no changes to the annual cycle, depending on time of year. This time-dependence can be shown systematically by plotting timing responses over the annual cycle. Such phase-response curves (Fig. 3A) or sensitivity profiles (Fig. 3B) have been described by studies of biological rhythms (DeCoursey 1960; Gwinner 1996b; Helm et al. 2009) and phenology time series (Thackeray et al. 2016), respectively.

Figure 3A shows the response of female reproductive timing (follicle growth) to long days in captive Garden Warblers (*Sylvia borin*) (Gwinner 1996b). This usually single-brooded species responds to long days in summer with a shut-down of the reproductive system. Subsequently, reproductive responsiveness is low over winter, but in spring garden warblers respond to long days with reproductive activation and advance their annual cycle. A downregulated response is important for migratory species which in their winter quarters experience conditions that may induce breeding (Hamner and Stocking 1970; Gwinner 1996b; Helm et al. 2009). To be sure to return to breeding sites in spring, rather than breed in the winter quarters, it is important to ignore potentially misleading cues at some times of year, while paying close attention to these cues at other times.

A recent, grand-scale study of phenology of wild species in the United Kingdom showed wide-spread, time-dependent sensitivity to ambient temperature and precipitation (Thackeray et al. 2016). The most common pattern was that prior to a phenological event (e.g. breeding), high temperature or precipitation advanced its timing. At earlier dates, response profiles were typically flat, and even earlier, high temperature or precipitation delayed events. Figure 3B shows the phase-dependent response of egglaying to ambient temperature in Barn Swallows (*Hirundo rustica*; Dario Massimino, pers. comm.; Thackeray et al. 2016). Barn Swallows show advance responses to high temperatures in spring and summer, followed by delay responses during autumn and winter. The broadly similar findings from captive and wild birds emphasize the relevance of phase-specific responses for seasonally appropriate behavior. Differences between the species, in turn, may be due to the more flexible annual behaviors of Barn Swallows. It might be no coincidence that in Barn Swallows, recent cross-hemispheric colonization was observed, associated with complete inversion of the annual cycle (Winkler et al. 2017). Such an inversion is easy to envision if some individuals become sensitive to long and warm days while still on the winter grounds.

Differences between species in response-profiles have important implications for the ability of birds to respond to climate change. Strongly migratory species typically differ from residents by lower flexibility in response to spring cues (Phillimore et al. 2016). Figure 3C shows schematically how flexibility of migrants is specifically reduced in winter compared to resident species. Because of this programming

difference, which has likely been adaptive, migrants may now be constrained in their ability to flexibly adjust annual cycles, and instead require evolutionary change (Phillimore et al. 2016). That such change may be possible has recently been shown for Pied Flycatchers (*Ficedula hypoleuca*; Helm et al. 2019). In this study, a full-annual cycle experiment on captive birds was replicated after 21 years, over which period a wild population had been continuously monitored. Spring activities of both, captive and wild birds, advanced at similar rates (9 and 11 days in 21 years, respectively). In the captive birds, where the full annual cycle was monitored, this advancement occurred selectively during the late winter and early spring phases, suggesting evolutionary acceleration of the circannual clock during winter (Helm et al. 2019).

Diel timing: Migratory flights in many species occur at night, implying a seasonal change in individuals from almost exclusively daytime activity to nocturnal flight. This shift to additional nocturnality is starkly detectable in the wild, for example on a continental scale using weather radars (Horton et al. 2020), and in captivity as migratory restlessness as described above. Recent studies have indeed indicated that strong Zugunruhe associates with higher probability to migrate in the wild (Eikenaar et al. 2014; Mukhin et al. 2018). However, wild and captive birds also show differences in the extent of night activity during migration seasons. For example, whereas wild birds intersperse migration nights between several nights of rest, captive birds typically show restlessness on most nights of the migration seasons (Åkesson et al. 2017).

Shifts to nocturnality during migration seasons are puzzling, given that in birds and most other organisms, day-night rhythms are stably organized by circadian clocks (Helm et al. 2017; Fig. 4). Experimental studies on several species of songbirds have shown that Zugunruhe is, however, organized as part of the avian circadian system, rather than supplanting it (Bartell and Gwinner 2005; Kumar et al. 2006; Coppack et al. 2008; Coverdill et al. 2008; Mukhin et al. 2018). For example, bouts of Zugunruhe, recognizable by extensive flight behavior, recur rhythmically even under experimental conditions when birds are fully sheltered from environmental information (i.e., receiving continuous dim light, constant temperature and food availability). Several studies have suggested that the birds' circadian system contains at least two internal drivers of rhythms (i.e., oscillators), of which one produces diurnal and the other

nocturnal activity (Bartell and Gwinner 2005; Mukhin et al. 2018). For much of the year, output from the day-time driver dominates, but during migration seasons, the night-time driver's activity becomes discernible. The location and functional details of the oscillators driving daytime and nighttime activity are not yet resolved. The avian circadian system consists of several pacemakers (Fig. 4) that are interconnected, and are in turn sensitive to multiple environmental sensory inputs as well as to signalling from within the body (Kumar et al. 2006; Cassone 2014; Helm et al. 2017). The particular responsiveness of Zugunruhe (see 4.2) to food availability suggests links of the Zugunruhe oscillator to metabolic signals, and perhaps to brain circuits that are part of the award system (Bartell and Gwinner 2005; Horton et al. 2019).

3.2. Space

Birds tend to follow inherited species- and population-specific migration routes (e.g. Helbig et al. 1996, Willemoes et al. 2014), which will lead them to suitable stop-over and wintering areas (Fransson et al. 2005, Newton 2008). The endogenous programs guiding young birds encode compass and space information in relation to the internal clock (Berthold 1996, Gwinner 1996ab, Able 1980, Åkesson et al. 2014). The three biological compasses used by migratory birds are based on information from the sun and the skylight polarization pattern, stars and the geomagnetic field (e.g. Wiltschko and Wiltschko 1972, Emlen 1975, Able 1980, Schmidt-Koenig 1990, Åkesson et al. 2014), and their use is tightly connected to the diel and circannual time sense. The sun compass has a time-compensation mechanism enabling compensation for the apparent movement of sun across the sky (Schmidt-Koenig 1990, Schmidt-Koenig et al. 1991), while the stellar compass encodes direction towards geographic north based on the rotation center of the sky independent of time of day (Emlen 1967, 1970). The magnetic compass is expressed relative to the angle of inclination providing directions along a north-south axis towards and away from the poles without direct diel time input for its functionality (Wiltschko and Wiltschko 1972), but changes of courses are expressed at relevant times of year (e.g. Gwinner and Wiltschko 1978, Wiltschko and Wiltschko 1992). Perception of the magnetic field seems dependent on specialized photoreceptors activated by a limited range of wavelengths of light involving cryptochrome molecules (Ritz et al. 2009, Muheim et al. 2014). Compass interactions may further lead to recalibrations during migration

(e.g. Cochran et al. 2004, Muheim et al. 2006; cf. Åkesson et al. 2015), while during ontogeny a combined experience of geomagnetic information and a rotating star pattern is crucial for birds to express a relevant population-specific migratory direction at the right time of year (Weindler et al. 1996).

Once migrants have started their journey, simple compass mechanisms can sometimes explain the routes they follow (e.g. Kiepenheuer 1984, Alerstam and Pettersson 1991, Muheim et al. 2003, 2018, Åkesson and Bianco 2016; cf. Sokolovskis et al. 2018). For instance, long-distance bird migrants have been proposed to set a course at sunset or sunrise and follow it relative to the position of the sun as they cross longitudes using their time-compensated sun compass without readjusting it for local time during flight (Alerstam and Pettersson 1990; Alerstam et al. 2001). This mechanism has gained some support from radar observations of long-distance migrating arctic waders (Alerstam et al. 2001). Birds could also use their geomagnetic compass (i.e. inclination compass; Wiltschko and Wiltschko 1972), and keep track of the apparent inclination angle during long continuous flights, i.e. following magnetoclinic routes (Kiepenheuer 1984), in many cases leading birds along realistic migration routes as confirmed by tracking data (Åkesson and Bianco 2016, 2017). Especially challenging situations are met by using any of the alternative compasses in high arctic regions (e.g. Åkesson et al. 2001a, Muheim et al. 2003, 2018, Åkesson and Bianco 2016). Recently, a comparative study evaluating route simulations demonstrated potential use across the widest latitudinal range for the magnetic compass (i.e. magnetoclinic route; Åkesson and Bianco 2017).

An increasing number of bird tracking studies have revealed complex course changes throughout the annual cycle (e.g. Sutherland 1998, Berthold et al. 2004, Åkesson et al. 2012, Willemoes et al. 2014). Such complex routes, involving one or more shifts during migration (Helbig et al. 1989, Willemoes et al. 2014), raise the question of how course shifts are encoded relative to the circannual program in different species and populations of birds. We find experimental support for course shifts expressed at expected times under constant environmental conditions (Gwinner and Wiltschko 1978). In turn, there is evidence that geomagnetic information also affects the migration program. For example, expression of a relevant course shift required in some species exposure to the geomagnetic information

expected at specific latitudes along the migration route (Beck and Wiltschko 1982, 1988).

Geomagnetic information has also been shown to prompt ecophysiological changes, leading to increased mass increase in response to magnetic parameters associated with sites just in front of a large barrier. These findings, first shown in juvenile Thrush Nightingales (*Luscinia luscinia*; Fransson et al. 2001), suggest that this response is inherited and encoded in the endogenous migration program. For course shifts and refuelling, the endogenous circannual time program seems to be involved in controlling the timing of events and in determining a seasonally correct response to geomagnetic information (Kullberg et al. 2003, 2007, Henshaw et al. 2008). These findings strongly suggest that geomagnetic cues can trigger, advance or delay phases of the migration program, reminiscent of its responsiveness to daylength (Fig. 2).

In research on spatial programs, consideration of ontogenetic effects, usually captured by distinquishing naive from experienced migrants, has provided important insights. Whereas the navigational abilities described above hold for all age groups, adherence to the inherited migration program is typically strong in first-time migrants, but may thereafter be supplanted by experience. This has been shown repeatedly in displacement experiments, in which naive migrants followed the blueprint of the inherited program, whereas adults navigated to goal areas they had previously visited. The documented ability to correct for longitudinal displacements of adult birds (Perdeck 1958, Åkesson et al. 2005, Thorup et al. 2007, Kishkinev et al. 2015), remains to be further explored in juveniles (cf. Åkesson et al. 2005).

3.3. Variation in migration programs

Variation between individuals and populations in the timing program and its response profile to environmental factors (Figs. 2, 3) can take several forms. Individuals can differ from each other in the timing of some phases of the annual cycle, but then resynchronize during a specific phase (see 3.1). Alternatively, individuals or populations may show shifted timing of the entire annual cycle, as documented for two populations of Collared Flycatchers (*Ficedula albicollis*) (Briedis et al. 2016). The perhaps most extreme example is the full inversion of the annual cycle in Barn Swallows that colonized the southern hemisphere (Winkler et al. 2017).

Several mechanisms underlie changes in the timing program. If timing is consistent within individuals (i.e., individuals displaying different chronotypes), differences may have a genetic basis. Genetic differences can selectively affect specific phases of the annual cycle. For example, heightened light sensitivity of the reproductive axis (Ramenofsky 2011; Watts et al. 2018) may advance the timing of spring but not autumn migration, and advanced circannual timing under selection for early breeding occurred specifically in late winter and spring (Helm et al. 2019). Another possibility are epigenetic changes, e.g. methylation of genes involved in biological rhythms (Merlin and Liedvogel 2019). Ontogenetic effects, such as daylength at birth, affect timing mechanisms in mammals (e.g. Ciarleglio et al. 2011), and may do so also in birds. Additional variation within and between populations may arise from flexible responses to environmental factors that do not change the timing program, but modify its output (see below).

Variation in spatial programs can arise from different sources. Classical studies, notably experiments with European Blackcaps (*Sylvia atricapilla*) have emphasised genetic determination of directional preference and duration of migratory restlessness (Berthold and Querner 1981, Berthold et al. 1992, Helbig1996). Such polyphenisms are now used in comparative genomic studies aimed at revealing the genetic underpinnings of migration (e.g. Liedvogel et al. 2011, Lundberg et al. 2017). The studies will be important to identify genes involved in encoding variations in space, time and fueling, but also how these genes expressed during migration are regulated.

For individual variation in orientation capacity and compass route-following, the underlying reasons may be related to the perception of the celestial and geomagnetic cues themselves (Muheim et al. 2014), as well as how these cues are encoded in the endogenous migration program. However, we still need to understand exactly how the endogenous migration program interacts with external information, and how birds keep track of space during long migrations throughout the annual cycle. A successful research agenda may be to combine an experimental approach (e.g. Kishkinev et al. 2015, Willemoes et al. 2015, Wikelski et al. 2015, Ilieva et al. 2018) with advanced tracking in the wild (e.g. Willemoes et al. 2014, Bäckman et al. 2017, Sokolovskis et al. 2018, Norevik et al. 2019).

Variation within the population can reveal interesting characteristics, where interactions of the inherited migration phenotype with different environmental factors can lead to the evolution of diverse migration patterns. Phenotypic plasticity may for example lead to advancement of migration timing in response to environmental conditions, in particular in flock-migrating birds (Fraser et al. 2019). Populations may furthermore comprise migratory and resident fractions (i.e. partial migration), or migration may differ between sex and age classes (i.e. differential migration) (Terrill and Able 1988, Newton 2008). In partial migration, individual phenotypes may range from completely sedentary to completely migratory (Chapman et al. 2011). Partial and differential migration systems thus enable investigation of effects of selection pressures and fitness consequences of different migration strategies, in particular in long-lived species (Gaillard 2013; Reid et al. 2018). In different species, this variation can be based on different mechanisms. For example, in European Blackcaps migratory phenotype appears to have a strongly genetic basis (i.e. polyphenism) (Pulido and Berthold 2010), and in Northern Wheatears (*Oenanthe oenanthe;* Maggini and Bairlein 2012) and Dark-eyed Juncos (*Junco hyemalis*; Holberton 1993), differences between the sexes are part of the circannual program. In other species, for example Stonechats, differences between migrants and residents are partly environmentally induced (Van Doren et al. 2017). While for most species contributions of genes and environment are unknown, it is likely that both factors are involved.

3.4. Mechanistic integration

Physiological studies, which are beyond the scope of this review, have provided a general picture of the mechanisms of migration programs, although details are still largely unclear. Figure 4 summarizes these findings with an emphasis on timing. It shows schematically how information from the environment affects components of the biological clock that drives the migration program. Spatial cues may also be integrated at this stage. This information is processed in the brain, affects the clock, and prompts a response that is specific to the phase of the annual cycle (Fig. 3). Effector systems then fine-tune behavioural and physiological responses by integrating information from within the bird (e.g. its energetic or health state) and from the immediate environment (e.g. weather, food availability) via hormonal pathways

(Ramenofsky 2011; Goymann et al. 2017; Watts et al. 2018). Ultimately, synthetization of this information leads to spatio-temporal migration behaviour and physiology. The migration program itself can be modified via genetic change, during ontogeny, and epigenetically.

4. Programmed flexibility in response to environmental factors

Within the time window set by the program for migration, decisions about its implementation are sensitive to a range of environmental factors that determine successful migration (Fig. 4). Departure time may be adjusted in response to level of fuel reserves, and relative to the expected onward migration route, including distance of barrier crossings (Müller et al. 2018). Responses to these environmental factors are partly inherited, and therefore, we here expand on their effects. We consider some other aspects of flexibility, for example learning, social behaviour and responses to weather, to represent residual flexibility.

4.1. Adjusting the drive to migrate in response to food

An important feature of migration is the capacity to prepare for prolonged migratory flights by fueling at stopover sites (Åkesson and Hedenström 2007). In fact, birds are predicted to spend 1:7 parts of migration time on flight and refueling at stopover, respectively (Hedenström and Alerstam 1998). Timing and extent of fuelling events may be encoded in the endogenous program in relation to expected flight distances (e.g. Fransson et al. 2001, Kullberg et al. 2007), but may also be modified in response to environmental conditions met during flight as well as at stopover sites.

The duration of stop-over, when migrants rest at night, can be predicted by a bird's body reserves, both in the field (Goymann et al. 2010) and in captivity (Gwinner 1996a, Gwinner et al. 1988): with increasing reserves, birds are more likely to depart, or to show high levels of Zugunruhe (i.e. migratory drive), respectively. However, this relationship only holds when sufficient local food is available. When food is scarce or inaccessible, birds show the opposite behaviour, departing, or showing particularly high Zugunruhe, on low fuel stores (Gwinner et al. 1988). Figure 5 shows how this behaviour interacts with the migration program in a series of experiments on garden

warblers (Gwinner et al. 1988). In September, during main autumn migration, Zugunruhe was high. When food was temporarily removed, the birds responded by increased night activity (I in Fig. 5). On return of *ad libitum* food, the birds paused Zurunruhe while refeeding (P in Fig. 5), and resumed Zugunruhe after regaining body mass (R in Fig. 5). In winter, after Zugunruhe had naturally stopped, it was reactivated by food reduction and immediately stopped after food return. These studies show that food availability affects movement decisions of birds during and outside migration seasons, presumably via endocrine pathways (Goymann et al. 2017). The food-induced changes had no effect on the overall migration program of the study birds (Gwinner 1996a), but likely modify a bird's actual migration.

4.2. Adjusting the drive to migrate and fuelling in response to geomagnetic cues

Migratory restlessness can be modified by exposure to geomagnetic field parameters expected to be met en route or at destination areas. This insight, which was previously shown for nocturnally migrating Northern Wheatears (Bulte et al. 2017), was recently also experimentally revealed for diurnally migrating Dunnocks (*Prunella modularis*) (Ilieva et al. 2018). Migratory restlessness was recorded for individual Dunnocks during a two-week period, during which one group was kept in the local Swedish geomagnetic field, while two other groups were geomagnetically displaced north (away from wintering area) or south (towards the wintering area in southern France) (Ilieva et al. 2018). The birds showed two peaks of activity throughout the 24h-cycle, with the longest peak in the morning, associated with migration, and a shorter evening peak associated primarily with feeding (Ilieva et al. 2018). The Dunnocks displaced south reduced the morning migratory restlessness as they were exposed to the geomagnetic parameters, i.e. inclination angle and total field intensity, at the wintering area, while the control birds instead increased the migratory restlessness over the study period (Fig. 6; Ilieva et al. 2018). The northern displacement resulted in continued, but somewhat reduced migration activity, suggesting it was not only the magnetic change itself, but also the characteristics of the magnetic parameters (i.e. combination of inclination and total field intensity at expected destination area), that interacted with the endogenous program resulting in

reduced migratory restlessness as the winter destination was geomagnetically reached (Ilieva et al. 2018). Like food availability, geomagnetic cues in this example appeared to modulate the output of the migration program, but at least within the study period, not the time course of it.

4.3. Adjusting directions in response to geomagnetic cues

Geomagnetic information can also modify the directional output of the migration program, but its effect differs between species. It is not completely understood why some species express a directional shift encoded with time as the migration season progresses (Gwinner and Wiltschko 1978), while orientation shifts by other species are only expressed by exposure to changes of geomagnetic information (Beck and Wiltschko 1988). To understand this we see a need for further studies of different bird species under controlled environmental conditions including magnetic displacements (e.g. Kishkinev et al. 2015).

Feed-back from geomagnetic information helps migratory birds meet a further challenge. Trans-hemispheric long-distance migrants are crossing the geomagnetic equator, which involves a 180°-shift of the angle of inclination, a key-feature of the birds' magnetic inclination compass (Wiltschko and Wiltschko 1972). Cage experiments with two long-distance migrating songbirds, the European Garden Warbler and the North American Bobolink (*Dolichonyx oryzivorus*), have revealed that these birds possess inherited responses where they adaptively change their preferred orientation with respect to the inclination angle, as they are exposed to a horizontal magnetic field simulating a magnetic equator crossing (Wiltschko and Wiltschko 1992, Beason 1992). It would be interesting to investigate if this response to magnetic inclination by shifting courses is present in most avian migrants, or if it is characteristic for the long-distance migrants adapted to trans-hemisphere flights.

Once terrestrial birds have initiated migration they may cross landmasses, but also barriers such as seas, mountains and deserts, where they may be unable to land. The inhospitable terrain may challenge their migration performance and stopover use during migration, leading to special adaptations (Åkesson and Hedenström 2007). At coastal sites, in particular, young birds may hesitate to continue on a sea-crossing

and are grounded in large numbers. They may then search for foraging sites and shelter (Alerstam 1978), and perform reverse migration to inland sites before they continue in the migration direction several days later (e.g. Åkesson et al. 1996a). Temporary reverse migration is typically expressed near coastal barriers leading to more suitable stop-over sites (Åkesson et al. 1996a, Zehnder et al. 2002, Buler and Moore 2011), whereas at inland locations reverse migration is less common (Åkesson 1999, Komenda-Zehnder et al. 2002). Temporary reverse migration and movements to nearby stopover sites are predominantly found in birds with low fuel reserves (Åkesson et al. 1996a, Sandberg 2003, Covino et al. 2015), and its directions are expressed in relation to the geomagnetic field (Sandberg 1994, Bäckman et al. 1997). Thus, as shown for effects of food shortage and magnetic cues on migratory drive, adaptive responses to barriers seem to be embedded in the migration program.

5. Flexibility residual to the migration program

Some aspects of flexibility have no clear relationship with migration programs, or appear to contradict, override or supplant them. Major effects are exerted by weather and availability of favorable winds (e.g. Åkesson and Hedenström 2000, Åkesson et al. 2002, Shamoun-Baranes et al. 2007, Sjöberg et al. 2015, Eikenaar and Schmaljohann 2015, Van Doren and Horton 2018). Availability of celestial compass cues (Åkesson et al. 1996b, 2001b) and locations of suitable stopover sites may furthermore have a strong effect on individual route choices when crossing large barriers (Åkesson et al. 2016). A further contributing factor are social effects on migration (Helm et al. 2006). This underrated factor is beginning to be addressed by exciting new data from tracking studies. For example, a recent study on European Bee-Eaters (*Merops apiaster*) presented migration data from 29 individuals moving in different groups (Dhanjal-Adams et al. 2018). Timing within groups was closely coordinated, and once separated, groups rejoined each other within days, even after a transcontinental journey. These data indicate both strong social effects and a detailed migration program, which could be innate, learned, or resource driven.

Learning and development are forms of flexibility that are still poorly known. For most birds it is unknown how migration performance develops with time. There are

examples where adult birds have been shown to migrate faster (Ellegren 1993), cover longer flight paths per day (Weimerskirch et al. 2006), handle wind drift more efficiently (Thorup et al. 2003), follow shorter routes and have shorter stopover times (Crysler et al. 2016) than juvenile birds. A recent example from a long-term study documents all these parameters for individually tracked migratory Black Kites (*Milvus migrans*; Fig. 7A) across a time span of 1-27 years (Sergio et al. 2014). This study shows that the development of migratory behavior in young birds follows a consistent trajectory, and that the development is more gradual and prolonged than previously assumed (Fig. 7B,C). More efficient migration performance was further shown to be promoted by a combination of individual improvement across time and selective mortality occurring most frequently in early phases of life during the pre-breeding migration period (Sergio et al. 2014). Several migration components improved across time, including increased migration speed, shorter stopover time, and increased efficiency to handle cross-winds in adult birds as compared to juveniles (Sergio et al. 2014). The strongest selection occurred on the flanks of the distribution during the early stages of life. Individuals that were able to improve their ability to handle environmental conditions efficiently on migration and to depart progressively earlier than conspecifics, obtained higher breeding and survival rates, leading to a longer life span (Fig. 7C).

Residual flexibility can either increase, or decrease, variation between individuals in time and space. Tracking data show that in some species delays in timing of breeding and migration departure may be difficult to correct for at later stages of the annual cycle. For instance, migratory Eurasian Nightjars (*Caprimulgus caprimulgus*) tracked by geolocators reveal that individuals being late in their departure timing in autumn, will continue to be late throughout the annual cycle, while early birds continue to be early (Norevik et al. 2017; Fig. 8). It is currently unknown whether these effects persisted beyond the duration of the annual cycle, or whether birds were eventually synchronized, as discussed above (see 3.1). If differences indeed persisted, they could partly reflect individual differences in chronotype (i.e. polyphenism).

6. Illustrating extremes of variation in inherited spatiotemporal behaviour

The wide range of mechanisms reviewed above can produce highly divergent outcomes. Below, we use extremes of variation within populations, ranging from great consistency to massive differentiation, to illustrate the many axes of variation in migration programs.

6.1. Low within-population variation in cuckoos and willow warblers

An example of limited inter-individual variation of a rather complex migration and stopover program comes from satellite tracking of the Common Cuckoo (*Cuculus canorus*). Cuckoos use a largely fixed sequence of stopover sites and route directions throughout the non-breeding period (Willemoes et al. 2014, Hewson et al. 2016; Fig. 9A). Initially the adult birds tracked from northwestern Europe depart towards the southeast in autumn, and stopover in central northern and thereafter southeastern Europe, before they initiate the Sahara crossing on southerly courses (Fig. 9A). After the barrier crossing they make a prolonged stopover in eastern Sahel (Willemoes et al. 2014, Hewson et al. 2016; Fig. 9A). Later in the season they will proceed to wintering areas further to the south, from where they will initiate northerly movements, following a loop migration in spring via West Africa (Willemoes et al. 2014, Hewson et al. 2016; Fig. 9A). The Cuckoo's somewhat stereotypic sequence of flight steps and stopovers during the non-breeding period is expressed timely with the availability of food resources in the areas visited, and encoded in the endogenous program (Willemoes et al. 2013). The phenotypic expression of this complex spatio-temporal program, and apparent use of goal areas throughout the non-breeding period, open up questions on what specific information is used to identify those areas throughout the annual cycle, and how potentially external information may interact with the migration decisions and route choices. In a displacement experiment with adult cuckoos during autumn migration Willemoes et al. (2015) investigated the capacity to return to the normal migration route, stopover and wintering areas. The displaced adult cuckoos showed some individual variation in the strategy they used to return, but also a capacity to navigate across areas potentially new to them (Willemoes et al. 2015). Juvenile cuckoos have further been shown to migrate later, show larger scatter in route choice and perform migration at slower pace than adults, but still they have been confirmed to reach the expected wintering areas by following their endogenous migration program (Vega et al. 2016).

Another species with highly conserved migration routes are Willow Warblers (*Phylloscopus trochilus*) (Fig. 10). However, these routes are specific to subspecies (*P. t. trochilus, acredula, yakutensis*) within the species' vast breeding range in Northern Europe and Asia. Willow warblers, thus, represent an interesting example where the evolution of migration routes, speciation and range expansion may be investigated (Bensch et al. 2009, Lundberg et al. 2017). Thanks to miniaturization of tracking technology we are now able to document migration behavior in these smallest of songbirds from different parts of their range (Lerche-Jørgensen et al. 2017, Sokolovskis et al. 2018; Fig. 10), which opens up the possibility to record route constancy and migration timing for birds with known, locally differing, genotypes (Lundberg et al. 2017). Special attention is given to hybrid zones where individuals with different endogenous migration programs breed side by side and may cross-breed, possibly resulting in intermediate directions in hybrids (Helbig 1991, Delmore and Irwin 2014). The consistent, but locally differentiated routes of Willow Warblers, thus offer great opportunities for detailed studies of the genetic program encoding migration behaviour, and the phenotypic expression of it (Bensch et al. 2009, Ruegg et al. 2014) .

6.2. High within-population variation in plovers and albatrosses

Conversely, exceptional variation in migration directions, route choice and wintering areas is exemplified within one single study population of the Little Ringed Plover (*Charadrius dubius*) (Hedenström et al. 2013). In this population, birds breeding side by side within the same gravel pit may migrate to wintering areas from Nigeria in the west to India in the east (Hedenström et al. 2013; Fig. 9B). The extreme variation in inherited direction and longitudinal range of wintering area selection call for further understanding of the genetics behind the phenotypic expression of the migration program in birds like the Little Ringed Plover.

Another example for exceptionally high variation comes from partially migratory Wandering Albatross (*Diomedea exulans*), whose behaviour differs from conventional migration systems (Fig. 11). The Wandering Albatross is known for its long lifespan, oceanic lifestyle and for breeding on isolated sub-Antarctic Islands. Between reproductive events it spends a sabbatical year at sea before returning to its previous breeding island (Tickell 1968, Weimerskirch and Wilson 2000). In this

species, differential non-breeding movement strategies have evolved in populations with limited genetic differentiation (Milot et al. 2008). Birds from different breeding colonies may predominantly move to different ocean areas (Weimerskirch et al. 2015; Fig. 11). Young wandering albatrosses have further been shown to follow similar routes as adults during their first migration and to spend their first year in sex-specific ocean areas overlapping with the adults, with males moving over twice the distance of females, demonstrating endogenous control of area use (Åkesson and Weimerskirch 2014).

During the sabbatical year, adult wandering albatrosses follow three alternative movement strategies: sedentary, sedentary with excursions, or migratory (Weimerskirch et al. 2015; Fig. 11). The proportion of birds adhering to the different strategies may differ between colonies. Wandering Albatrosses at Kergulean Island are all migratory, while the sedentary strategy is present in Crozet Island birds (Weimerskirch et al. 2015; Fig. 11). The migratory strategy is furthermore more commonly used by males than by females (Wemerskirch et al. 2015), and differentially expressed already in young birds (Åkesson and Weimerskirch 2014). A sedentary strategy, predominantly used by females at Crozet Island, has increased in recent years (Weimerskirch et al. 2015), possibly as a consequence of climate change (Fryxell and Holt 2013), revealing a potential to adapt to new environmental conditions by phenotypic flexibility or as a consequence of natural selection. A long-term population change in movement strategies including settling down, may in turn lead to bird diversification and speciation as suggested by Rolland et al. (2014).

7. Conclusions and outlook

In this review, we have shown how in bird migration, inherited programs and responses to the environment interact. As in other fields of biology, it is time to leave behind old dichotomies between genetics and physiology on the one hand, and ecology on the other. Evolution has brought about an impressive range of solutions to the problem that migration requires both predictive anticipation and flexibility (Figs. 9 and 11). For some aspects of migration, we begin to understand the birds' flexibility on the basis of inherited reaction norms that provide solutions which were effective over evolutionary time. These insights refine views of environmental effects on migration, as being dependent on the phase of the annual cycle and a bird's

migration program (Figs. 3 and 5). They also refine views of carry-over effects as being at least in part permitted, or counter-acted, by migration programs (Fig. 2). The combined developments of molecular tools and tracking technology, if applied to rewarding model systems (e.g. Fig. 10), are set to greatly foster this understanding. For some other aspects, we currently do not know how decisions are made, and how migrants improve by learning. The study on Black Kites (Fig. 7) is one of the most informative about the development of migration performance in individual birds, but calls for follow-up studies on other species (Campioni et al. 2020), in particular those relying strongly on an endogenous program for their first migration. Likewise, the cited study on European Bee-Eaters (Dhanjal-Adams et al. 2018) offers exciting insights on migration of highly social species, which will hopefully be complemented by work on species with different social systems. In addition, recent findings from the European Nightjar call attention to yet another temporal domain that may have been largely overlooked, at least in landbirds. Nocturnally migratory nightjars time fueling and migration events to the different phases of the moon (Norevik et al. 2019), and thereby call for further studies of moon cycle effects on migratory birds, ideally with a circannual perspective (Chapin and Wing 1959; Cruz et al. 2013).

Ultimately, combined ecological and mechanistic studies may explain why some species strictly adhere to spatio-temporal programs whereas others are flexible, and how selection pressures, from competitive temporal niche segregation (Heim et al. 2018) to climate change, may shape migrations in the future. We hope that our overview will encourage future cross-over between approaches that focus on annual-cycle programs and those that focus on the environment, as jointly these components enable migratory birds to carry out their great journeys.

References

Able, K. P. (1980). Mechanisms of orientation, navigation and homing. In *Animal migration, orientation and navigation*, pp. 283-373. New York: Academic Press.

Åkesson, S. (1999). Do passerine migrants captured at an inland site perform temporary reverse migration in autumn? *Ardea* 87, 129-137.

Åkesson, S., and Bianco, G. (2016). Assessing vector navigation in long-distance migrating birds. *Behav. Ecol.* 27, 865-875.

Åkesson, S., and Bianco, G. (2017). Route simulations, compass mechanisms and long-distance migration flights in birds. *J. Comp. Physiol. A* 203, 475-490.

Åkesson, S., and Hedenström, A. (2000). Wind selectivity of migratory flight departures in birds. *Behav. Ecol. Sociobiol.* 47, 140-144.

Åkesson, S., and Hedenström, A. (2007). How migrants get there: Migratory performance and orientation. *BioScience* 57, 123-133.

Åkesson, S., and Weimerskirch, H. (2014). Evidence for sex-segregated ocean distributions of first-winter wandering albatrosses at Crozet Islands. *Plos one* 9, e86779.

Åkesson, S., Karlsson, L., Walinder, G., and Alerstam, T. (1996a). Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia. *Behav. Ecol. Sociobiol.* 38, 293-302.

Åkesson, S., Alerstam, T., and Hedenström, A. (1996b). Flight initiation of nocturnal passerine migrants in relation to celestial orientation conditions at twilight. *J. Avian Biol.* 27, 95-102.

Åkesson, S., Morin, J., Muheim, R., and Ottosson, U. (2001a). Avian orientation at steep angles of inclination: experiments with migratory white–crowned sparrows at the magnetic North Pole. *Proc. R. Soc. B.* 268, 1907-1913.

Åkesson, S., Walinder, G., Karlsson, L., and Ehnbom, S. (2001b). Reed warbler orientation: initiation of nocturnal migratory flights in relation to visibility of celestial cues at dusk. *Anim. Behav.* 61, 181-189.

Åkesson, S., Walinder, G., Karlsson, L., and Ehnbom, S. (2002). Nocturnal migratory flight initiation in reed warblers *Acrocephalus scirpaceus*: effect of wind on orientation and timing of migration. *J. Avian Biol.* 33, 349-357.

Åkesson, S., Klaassen, R., Holmgren, J., Fox, J. W., and Hedenström, A. (2012). Migration routes and strategies in a highly aerial migrant, the common swift *Apus apus*, revealed by light-level geolocators. *PloS one* 7(7), e41195.

Åkesson, S., Boström, J., Liedvogel, M., and Muheim, R. (2014). Animal navigation. In: Animal movement across scales (Eds. L.-A. Hansson and S. Åkesson), pp. 151-178. Oxford University Press.

Åkesson, S., Odin, C., Hegedüs, R., Ilieva, M., Sjöholm, C., Farkas, A., and Horváth, G. (2015). Testing avian compass calibration: comparative experiments with diurnal and nocturnal passerine migrants in South Sweden. *Biol. Open* 4, 35-47.

Åkesson, S., Bianco, G., and Hedenström, A. (2016). Negotiating an ecological barrier: crossing the Sahara in relation to winds by common swifts. *Phil. Trans. R. Soc. B* 371(1704), 20150393.

Åkesson, S., Ilieva, M., Karagicheva, J., Rakhimberdiev, E., Tomotani, B., and Helm, B. (2017). Timing avian long-distance migration: From internal clock mechanisms to global flights. *Phil. Trans. R. Soc. B* 372, 372, 1734.

Åkesson, S., Morin, J., Muheim, R., and Ottosson, U. (2005). Dramatic orientation shift of white-crowned sparrows displaced across longitudes in the high arctic. *Curr. Biol.* 15, 1591-1597.

Alerstam, T. (1978). Reoriented bird migration in coastal areas: dispersal to suitable resting grounds?. *Oikos* 30, 405-408.

Alerstam, T., and Lindström, Å. (1990). Optimal bird migration: the relative importance of time, energy, and safety. In *Bird migration* (pp. 331-351). Springer, Berlin, Heidelberg.

Alerstam, T., and Pettersson, S. G. (1991). Orientation along great circles by migrating birds using a sun compass. *J. Theor. Biol.* 152, 191-202.

Alerstam, T., Gudmundsson, G. A., Green, M., and Hedenström, A. (2001). Migration along orthodromic sun compass routes by arctic birds. *Science* 291, 300-303.

Altshuler, D. L., Cockle, K. L., and Boyle, W. A. (2013) North American ornithology in transition. *Biol. Lett.* 9, 20120876.

Bäckman, J., Andersson, A., Alerstam, T., Pedersen, L., Sjöberg, S., Thorup, K., et al. (2017). Activity and migratory flights of individual free-flying songbirds throughout the annual cycle: method and first case study. *J. Avian Biol.* 48, 309-319.

Bäckman, J., Pettersson, J., and Sandberg, R. (1997). The influence of fat stores on magnetic orientation in day-migrating Chaffinch, *Fringilla coelebs*. *Ethology* 103, 247-256.

Barlow, R. B., Powers, M. K., Howard, H., and Kass, L. (1986). Migration of Limulus for Mating: Relation to Lunar Phase, Tide Height, and Sunlight. *Biol. Bull.* 171, 310-29.

Bartell, P. A. and E. Gwinner (2005). A Separate Circadian Oscillator Controls Nocturnal Migratory Restlessness in the Songbird *Sylvia borin*. *J. Biol. Rhythms* 20, 538-549.

Beason, R. C. (1992). You can get there from here: responses to simulated magnetic equator crossing by the bobolink (*Dolichonyx oryzivorus*). *Ethology* 91, 75-80.

Beck, W., and Wiltschko, W. (1982). The magnetic field as a reference system for genetically encoded migratory direction in pied flycatchers (*Ficedula hypoleuca* Pallas). *Z. Tierpsychol.* 60, 41-46.

Beck, W., and Wiltschko, W. (1988). Magnetic factors control the migratory direction of pied flycatchers (*Ficedula hypoleuca,* Pallas). *Acta XIX Congr. Int. Ornithol. Ottawa* 1986, 1955–1962.

Bensch, S., Grahn, M., Müller, N., Gay, L., and Åkesson, S. (2009). Genetic, morphological, and feather isotope variation of migratory willow warblers show gradual divergence in a ring. *Mol. Ecol.* 18, 3087-3096.

Berthold, P. (1973). Relationships between migratory restlessness and migration distance in six Sylvia species. *Ibis* 115, 594-599.

Berthold, P. (1996). Control of Bird Migration. London: Chapman & Hall.

Berthold, P., and Querner, U. (1981). Genetic basis of migratory behavior in European warblers. *Science* 212, 77-79.Berthold, P., Helbig, A. J., Mohr, G., and Querner, U. (1992). Rapid microevolution of migratory behaviour in a wild bird species. *Nature* 360, 668–670.

Berthold, P., Kaatz, M., and Querner, U. (2004). Long-term satellite tracking of white stork (*Ciconia ciconia*) migration: constancy versus variability. *J. Ornithol.* 145, 356-359.

Bertin, A., Houdelier, C., Richard-Yris, M.-A., Guyomarc'h, C., and Lumineau, S. (2007). Stable Individual Profiles of Daily Timing of Migratory Restlessness in European Quail. *Chronobiol. Int.* 24: 253-267.

Birkhead, T.R. (2008). *The Wisdom of Birds. An illustrated history of ornithology.* Vol. pp. Bloomsbury, London.

Briedis, M., Hahn, S., Gustafsson, L., Henshaw, I., Träff, J., Král, M., et al. (2016). Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant. *J. Avian Biol.* 47, 743-748.

Briedis, M., Krist, M., Král, M., Voigt, C. C., and Adamík, P. (2018). Linking events throughout the annual cycle in a migratory bird—non-breeding period buffers accumulation of carry-over effects. *Behav. Ecol. Sociobiol.* 72, 93.

Bojarinova, J., and Babushkina, O. (2015). Photoperiodic conditions affect the level of locomotory activity during autumn migration in the Long-tailed Tit (*Aegithalos c. caudatus*). *Auk* 132, 370-379.

Budki, P., Rani, S., and Kumar, V. (2009). Food deprivation during photosensitive and photorefractory life-history stages affects the reproductive cycle in the migratory Red-headed Bunting (*Emberiza bruniceps*). *J. Exp. Biol.* 212, 225-230.

Buler, J. J., and Moore, F. R. (2011). Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. *J. Ornithol.* 152, 101-112.

Bulte, M., and Bairlein, F. (2013). Endogenous control of migratory behavior in Alaskan northern wheatears *Oenanthe oenanthe*. *J. Ornithol.* 154, 567-570.

Bulte, M., Heyers, D., Mouritsen, H., and Bairlein, F. (2017). Geomagnetic information modulates nocturnal migratory restlessness but not fueling in a long distance migratory songbird. *J. Avian Biol.* 48, 75-82.

Campioni, L., Dias, M. P., Granadeiro, J. P., and Catry, P. (2020). An ontogenetic perspective on migratory strategy of a long-lived pelagic seabird: Timings and destinations change progressively during maturation. *J. Anim. Ecol.* 89, 29–43.

Carneiro, C., Gunnarsson, T. G., and Alves, J. A. (2019). Why Are Whimbrels Not Advancing Their Arrival Dates Into Iceland? Exploring Seasonal and Sex-Specific Variation in Consistency of Individual Timing During the Annual Cycle. *Frontiers Ecol. Evol* 7, 248.

Cassone, V. M. (2014). Avian Circadian Organization: A Chorus of Clocks. *Frontiers Neuroendocrinol.* 35, 76-88.

Chan, K. (1995). Diurnal and nocturnal pattern of activity in resident and migrant Silvereyes *Zosterops lateralis*. *Emu* 95, 41–46.

Chapin, J. P. and L. W. Wing (1959). The Wideawake Calendar, 1953 to 1958. *Auk* 76, 153-158.

Chapman, B. B., Brönmark, C., Nilsson, J.-Å., and Hansson, L.-A. (2011). The ecology and evolution of partial migration. *Oikos* 120, 1764-75.

Ciarleglio, C. M., Axley, J. C., Strauss, B. R., Gamble, K. L., and McMahon, D. G. (2011). Perinatal photoperiod imprints the circadian clock. *Nature Neurosci.* 14, 25-27.

Cochran, W. W., Mouritsen, H., and Wikelski, M. (2004). Migrating songbirds recalibrate their magnetic compass daily from twilight cues. *Science* 304, 405-408.

Conklin, J. R., Battley, P. F., and Potter, M. A. (2013) Absolute Consistency: Individual versus Population Variation in Annual-Cycle Schedules of a Long-Distance Migrant Bird. *PLoS One* 8, e54535.

Conklin, J. R., Battley, P. F., Potter, M. A., and Fox, J. W. (2010). Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. *Nature Comm.* 1,67.

Coppack, T., S. F. Becker and P. J. J. Becker (2008). Circadian flight schedules in night-migrating birds caught on migration. *Biol. Lett.* 4, 619-622.

Coverdill, A. J., Bentley, G. E., and Ramenofsky, M. (2008). Circadian and Masking Control of Migratory Restlessness in Gambel's White-Crowned Sparrow (*Zonotrichia leucophrys gambelii*). *J. Biol. Rhythms* 23, 59-68.

Covino, K. M., Holberton, R. L., and Morris, S. R. (2015). Factors influencing migratory decisions made by songbirds on spring stopover. *J. Avian Biol.* 46, 73-80.

Cruz, S. M., Hooten, M., Huyvaert, K. P., Proaño, C. B., Anderson, D. J., Afanasyev, V., et al. (2013). At–Sea Behavior Varies with Lunar Phase in a Nocturnal Pelagic Seabird, the Swallow-Tailed Gull. *PLoS one* 8(2), e56889.

Crysler, Z. J., Ronconi, R. A., and Taylor, P. D. (2016). Differential fall migratory routes of adult and juvenile Ipswich Sparrows (*Passerculus sandwichensis princeps*). *Movem. Ecol.* 4, 3.

DeCoursey, P. (1960). Daily light sensitivity rhythm in a rodent. *Science* 131, 33-35.

DeCoursey, P. (2004). The Behavioral Ecology and Evolution of Biological Timing Systems. In *Chronobiology: Biological Timekeeping*. Dunlap JC, Loros JJ, and Decoursey P (eds.), pp. 27-65. Sinauer, Sunderland MA.

Delmore, K. E., and Irwin, D. E. (2014). Hybrid songbirds employ intermediate routes in a migratory divide. *Ecol. Lett.* 17, 1211.

Dhanjal-Adams, K. L., Bauer, S., Emmenegger, T., Hahn, S., Lisovski, S., and Liechti, F. (2018). Spatiotemporal group dynamics in a long-distance migratory bird. *Curr. Biol.* 28, 2824-2830.

Eikenaar, C., and Schmaljohann, H. (2015). Wind conditions experienced during the day predict nocturnal restlessness in a migratory songbird. *Ibis* 157, 125-132.

Eikenaar, C., Klinner, T., Szostek, K. L., and Bairlein, F. (2014). Migratory restlessness in captive individuals predicts actual departure in the wild. *Biol. Lett.* 10(4).

Ellegren, H. (1993). Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. *Ornis Scand.* 24, 220–8.

Emlen, S. T. (1967). Migratory orientation in the Indigo Bunting, *Passerina cyanea*. Part II: mechanism of celestial orientation. *Auk* 84,463–489.

Emlen, S. T. (1970). Celestial rotation: its importance in the development of migratory orientation. *Science* 170, 1198–1202.

Emlen, S. T. (1975). Migration: orientation and navigation. In *Avian biology* (pp. 129-219). Academic Press.

Fransson, T., Jakobsson, S., Johansson, P., Kullberg, C., Lind, J., and Vallin, A. (2001). Bird migration: Magnetic cues trigger extensive refuelling. *Nature* 414, 35-36.

Fransson, T., Jakobsson, S., and Kullberg, C. (2005). Non-random distribution of ring recoveries from trans-Saharan migrants indicates species-specific stopover sites. *J. Avian Biol.* 36, 6-11.

Fraser, K. C., Shave, A. C., de Greef, E., Siegrist, J., and Garroway, C. J. (2019). Individual variability in migration timing can explain long-term, population-level advances in a songbird. *Frontiers Ecol. Evol*. 7, 324.

Friesen, V. L. (2015). Speciation in seabirds: why are there so many species…and why aren't there more? *J. Ornithol.* 156, 27-39.

Fryxell, J., and Holt, R. (2013). Environmental change and the evolution of migration. *Ecology* 94, 1274–1279.

Gaillard, J.-M. (2013). Assessing fitness consequences of migratory tactics requires longterm individually based monitoring. *Ecology* 94, 1261–1264.

Gill, J. A., Alves, J. A., Sutherland, W. J., Appleton, G. F., Potts, P. M., and Gunnarsson, T. G. (2014). Why is timing of bird migration advancing when individuals are not? *Proc. R. Soc. B* 281, 20132161.

Goymann, W., Lupi, S., Kaiya, H., Cardinale, M., and Fusani, L. (2017) Ghrelin affects stopover decisions and food intake in a long-distance migrant. *Proc. Natl. Acad. Sci.* USA 114, 1946-1951.

Goymann, W., Spina, F., Ferri, A., and Fusani, L. (2010) Body fat influences departure from stopover sites in migratory birds: evidence from whole-island telemetry. *Biol. Lett.* 6, 478-481

Goymann, W., Helm, B., Jensen, W., Schwabl, I., and Moore, I. T. (2012). A tropical bird can use the equatorial change in sunrise and sunset times to synchronize its circannual clock. *Proc. R. Soc. B* 279, 3527-3534.

Gow, E. A., Burke, L., Winkler, D. W., Knight, S. M., Bradley, D. W., Clark, R. G., et al. (2019). A range-wide domino effect and resetting of the annual cycle in a migratory songbird. *Proc. R. Soc. B* 286, 20181916.

Gwinner, E. (1986). *Circannual rhythms. Endogenous annual clocks in the organization of seasonal processes.* Berlin, Germany: Springer.

Gwinner, E. (1996a). Circadian and circannual programmes in avian migration. *J. Exp. Biol.* 199, 39-48.

Gwinner, E. (1996b) Circannual clocks in avian reproduction and migration. *Ibis* 138, 47-63.

Gwinner, E., and Wiltschko, W. (1978). Endogenously controlled changes in migratory direction of the Garden Warbler *Sylvia borin*. *J. Comp. Physiol. A* 125, 267-273.

Gwinner, E., and Wiltschko, W. (1980). Circannual changes in migratory orientation of the garden warbler, *Sylvia borin*. *Behav. Ecol. Sociobiol.* 7, 73-78.

Gwinner, E., Schwabl, H. and Schwabl-Benzinger, I. (1988). Effects of food-deprivation on migratory restlessness and diurnal activity in the garden warbler *Sylvia borin*. *Oecologia* 77, 321-326.

Häfker, N. S., Meyer, B., Last, K. S., Pond, D. W., Hüppe, L., and Teschke, M. (2017). Circadian Clock Involvement in Zooplankton Diel Vertical Migration. *Curr. Biol.* 27, 2194-2201.

Hamner, W. M., and Stocking, J. (1970). Why don´t Bobolinks breed in Brazil? *Ecology* 51, 743-751.

Hedenström, A., and Alerstam, T. (1998). How fast can birds migrate?. *J. Avian Biol.* 29, 424-432.

Hedenström, A., Klaassen, R. H., and Åkesson, S. (2013). Migration of the Little Ringed Plover *Charadrius dubius* breeding in South Sweden tracked by geolocators. *Bird Study* 60, 466-474.

Helbig, A. J. (1991). Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE-and SW-migrating blackcaps (*Sylvia atricapilla*). *Behav. Ecol. Sociobiol.* 28, 9-12.

Helbig, A. J. (1996). Genetic basis, mode of inheritance and evolutionary changes of migratory directions in Palearctic warblers (Aves: Sylviidae). *J. Exp. Biol.* 199, 49-55.

Helbig, A. J., Berthold, P., and Wiltschko, W. (1989). Migratory orientation in blackcaps (*Sylvia atricapilla*): population-specific shifts of direction during the autumn. *Ethology* 82, 307–315.

Heim, W., Eccard, J. A., and Bairlein, F. (2018). Migration phenology determines niche use of East Asian buntings (Emberizidae) during stopover. *Curr. Zool.* 64, 681-692.

Helm, B. (2006). Zugunruhe of migratory and non-migratory birds in a circannual context. *J. Avian Biol.* 37, 533-40.

Helm, B., and Gwinner, E. (2006). Migratory restlessness in an equatorial nonmigratory bird. *Plos Biology* 4, 611-4.

Helm, B., Gwinner, E. and Trost, L. (2005) Flexible seasonal timing and migratory behavior: Results from Stonechat breeding programs. *Ann. N.Y. Acad. Sci.* 1046, 216-227.

Helm, B., Piersma, T., and Van der Jeugd, H. (2006) Sociable schedules: interplay between avian seasonal and social behaviour. *Anim. Behav.* 72, 245-262.

Helm, B., Schwabl, I., and Gwinner, E. (2009). Circannual basis of geographically distinct bird schedules. *J. Exp. Biol.* 212, 1259-1269.

Helm, B., Van Doren, B. M., Hoffmann, D., and Hoffmann, U. (2019). Evolutionary Response to Climate Change in Migratory Pied Flycatchers. *Curr. Biol*. 29, 3714-3719.

Helm, B., Visser, M. E., Schwartz, W., Kronfeld-Schor, N., Gerkema, M., Piersma, T. et al. (2017). Two sides of a coin: ecological and chronobiological perspectives of timing in the wild. *Phil. Trans. R. Soc. B* 372, 20160246.

Helms, C. W. (1963). The annual cycle and Zugunruhe in birds. *Proceedings of the XIIIth International Ornithological Congress Ithaca*. Ithaca, American Ornithologists' Union: 925-939.

Henshaw, I., Fransson, T., Jakobsson, S., Lind, J., Vallin, A., and Kullberg, C. (2008). Food intake and fuel deposition in a migratory bird is affected by multiple as well as single-step changes in the magnetic field. *J. Exp. Biol.* 211, 649-653.

Hewson, C. M., Thorup, K., Pearce-Higgins, J. W., and Atkinson, P. W. (2016). Population decline is linked to migration route in the Common Cuckoo. *Nature Com.* 7, 12296.

Hodgson, S., and Quinn, T. P. (2002). The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. *Can. J. Zool.* 80, 542-55.

Holberton, R. L. (1993). An Endogenous Basis for Differential Migration in the Dark-Eyed Junco. *Condor* 95, 580-587.

Holberton, R. L., and Able, K. P. (1992). Persistence of circannual cycles in a migratory bird held in constant dim light. *J. Comp. Phys*. A 171, 477-481.

Horton, K. G., La Sorte, F. A., Sheldon, D., Lin, T.-Y., Winner, K., Bernstein, G., et al. (2020). Phenology of nocturnal avian migration has shifted at the continental scale. *Nature Clim. Change* 10, 63-68.

Horton, W. J., Jensen, M., Sebastian, A., Praul, C. A., Albert, I. and Bartell, P. A. (2019). Transcriptome Analyses of Heart and Liver Reveal Novel Pathways for Regulating Songbird Migration. *Sci. Rep*. 9, 6058.

Hut, R. A., and Beersma, D. G. M. (2011). Evolution of time-keeping mechanisms: early emergence and adaptation to photoperiod. *Phil. Trans. R. Soc. B* 366, 2141-54.

Ilieva, M., Bianco, G., and Åkesson, S. (2018). Effect of geomagnetic field on migratory activity in a diurnal passerine migrant, the dunnock, *Prunella modularis*. *Anim. Behav.* 146, 79-85.

Karagicheva, J., Rakhimberdiev, E., Dekinga, A., Brugge, M., Koolhaas, A., Ten Horn J. et al. (2016). Seasonal Time Keeping in a Long-Distance Migrating Shorebird. *J. Biol. Rhythms* 31, 509-21.

Kiepenheuer, J. (1984). The magnetic compass mechanism of birds and its possible associations with the shifting course direction of migrants. *Behav. Ecol. Sociobiol.* 14, 81-99.

King, J. R., and Farner, D. S. (1963). The Relationship of Fat Deposition to Zugunruhe and Migration. *Condor* 65, 200-223.

Kishkinev, D., Chernetsov, N., Pakhomov, A., Heyers, D., and Mouritsen, H. (2015). Eurasian reed warblers compensate for virtual magnetic displacement. *Curr. Biol.* 25, R822-R824.

Komenda-Zehnder, S., Liechti, F., and Bruderer, B. (2002). Is reverse migration a common feature of nocturnal bird migration?-an analysis of radar data from Israel. *Ardea* 90, 325-334.

Kramer, G. (1957). Experiments on bird orientation and their interpretation. *Ibis* 99, 196-227.

Kullberg, C., Henshaw, I., Jakobsson, S., Johansson, P., and Fransson, T. (2007). Fuelling decisions in migratory birds: Geomagnetic cues override the seasonal effect. *Proc. R. Soc. B* 274, 2145-2151.

Kullberg, C., Lind, J., Fransson, T., Jakobsson, S., and Vallin, A. (2003). Magnetic cues and time of season affect fuel deposition in migratory thrush nightingales (*Luscinia luscinia*). *Proc. R. Soc. B* 270, 373-378.

Kumar, V., Rani, S., and Singh, B. (2006). Biological clocks help reduce the physiological conflicts in avian migrants. *J. Ornithol.* 147, 281-286.

Lerche-Jørgensen, M., Willemoes, M., Tøttrup, A. P., Snell, K. R. S., and Thorup, K. (2017). No apparent gain from continuing migration for more than 3000 kilometres: willow warblers breeding in Denmark winter across the entire northern Savannah as revealed by geolocators. *Mov. Ecol.* 5, 17.

Liedvogel, M., Åkesson, S., and Bensch, S. (2011). The genetics of migration on the move. *Trends Ecol. Evol.* 26, 561-569.

Lundberg, M., Liedvogel, M., Larson, K., Sigeman, H., Grahn, M., Wright, A., et al. (2017). Genetic differences between willow warbler migratory phenotypes are few and cluster in large haplotype blocks. *Evol. Lett.* 1, 155-168.

Maggini, I., and Bairlein, F. (2010). Endogenous rhythms of seasonal migratory body mass changes and nocturnal restlessness in different populations of northern wheatear *Oenanthe oenanthe*. *J. Biol. Rhythms* 25, 268-276.

Maggini, I. and Bairlein, F. (2012) Innate Sex Differences in the Timing of Spring Migration in a Songbird. *PLoS One* 7, e31271.

McKinnon, L., Smith, P. A., Nol, E., Martin, J. L., Doyle, F. I., Abraham, K. F. et al. (2010). Lower Predation Risk for Migratory Birds at High Latitudes. *Science* 327, 326-327.

McKinnon, E. A., and Love, O. P. (2018). Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. *Auk* 135, 834-856.

Merlin, C., and Liedvogel, M. (2019). The genetics and epigenetics of animal migration and orientation: birds, butterflies and beyond. *J. Exp. Biol.* 222, jeb191890.

Milot, E., Weimerskirch, H., and Bernatchez, L. (2008). The seabird paradox: dispersal, genetic structure and population dynamics in a highly mobile, but philopatric albatross species. *Mol. Ecol.* 17, 1658–1673.

Muheim, R., Åkesson, S., and Alerstam, T. (2003). Compass orientation and possible migration routes of passerine birds at high arctic latitudes. *Oikos* 103, 341-349.

Muheim, R., Phillips, J. B., and Åkesson, S. (2006). Polarized light cues underlie compass calibration in migratory songbirds. *Science* 313, 837-839.

Muheim, R., Boström, J., Åkesson, S., and Liedvogel, M. (2014). Sensory mechanisms of animal orientation and navigation. In *Animal movement across scales* (pp. 179-194). Oxford University Press.

Muheim, R., Schmaljohann, H., and Alerstam, T. (2018). Feasibility of sun and magnetic compass mechanisms in avian long-distance migration. *Movem. Ecol.* 6, 8.

Mukhin, A., D. Kobylkov, D. Kishkinev and V. Grinkevich (2018). Interrupted breeding in a songbird migrant triggers development of nocturnal locomotor activity. *Sci. Rep.* 8, 5520.

Müller, F., Eikenaar, C., Crysler, Z. J., Taylor, P. D., and Schmaljohann, H. (2018). Nocturnal departure timing in songbirds facing distinct migratory challenges. *J. Anim. Ecol.* 87, 1102-1115.

Newton, I. (2008). *The migration ecology of birds.* Academic Press, London.

Norevik, G., Åkesson S, and Hedenström, A. (2017). Migration strategies and annual space-use in an Afro-Palaearctic aerial insectivore – the European nightjar *Caprimulgus europaeus*. *J. Avian Biol*. 48, 738–747.

Norevik, G., Åkesson, S., Andersson, A., Bäckman, J., and Hedenström, A. (2019). The lunar cycle drives migration of a nocturnal bird. *PLoS Biol*. 17(10).

van Noordwijk, A. J., Pulido, F., Helm, B., Coppack, T., Delingat, J., Dingle, H. et al. (2006). A framework for the study of genetic variation in migratory behaviour. *J. Ornithol.* 147, 221-233.

O'Connor, C. M., Norris, D. R., Crossin, G. T., and Cooke, S. J. (2014). Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere* 5, art28.

O'Connor, E. A., Cornwallis, C. K., Hasselquist, D., Nilsson, J. Å., and Westerdahl, H. (2018). The evolution of immunity in relation to colonization and migration. *Nature Ecol. Evol.* 2, 841.

Perdeck, A. C. (1958). Two types of orientation in migrating starlings, *Sturnus vulgaris* L., and chaffinches, *Fringilla coelebs* L., as revealed by displacement experiments. Ardea 55, 194-202.

Phillimore, A. B., Leech, D. I., Pearce-Higgins, J. W. and Hadfield, J. D. (2016). Passerines may be sufficiently plastic to track temperature-mediated shifts in optimum lay date. *Global Change Biol.* 22, 3259-3272.

Piersma, T., and Drent. J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends Ecol. Evol.* 18, 228–33.

Pulido, F. and Berthold, P. (2010) Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. *Proc. Natl. Acad. Sci.* USA 107, 7341-7346.

Ramenofsky, M. (2011). Hormones in migration and reproductive cycles of birds. In: Norris, David O., and Lopez, Kristin H. (eds.). *Hormones and reproduction of vertebrates*, Academic Press (London): pp. 205-237..

Reid, J. M., Travis, J. M. J., Daunt, F., Burthe, S. J., Wanless, S., and Dytham, C. (2018). Population and evolutionary dynamics in spatially structured seasonally varying environments. *Biol. Rev.* 93, 1578-603.

Reppert, S. M., and de Roode, J. C. (2018). Demystifying monarch butterfly migration. *Curr. Biol.* 28, R1009-R1022.

Ritz, T., Wiltschko, R., Hore, P. J., Rodgers, C. T., Stapput, K., Thalau, P., et al. (2009). Magnetic compass of birds is based on a molecule with optimal directional sensitivity. *Biophys. J.* 96, 3451-3457.

Rolland, J., Jiguet, F., Joansson, K. A., Condamine, F. L., and Morlon, H. (2014). Settling down of seasonal migrants promotes bird diversification. *Proc. R. Soc. B* 281, 20140473.

Ruegg, K., Anderson, E. C., Boone, J., Pouls, J., and Smith, T. B. (2014). A role for migration-linked genes and genomic islands in divergence of a songbird. *Mol. Ecol.* 23, 4757-4769.

Sandberg, R. (1994). Interaction of body condition and magnetic orientation in autumn migrating robins, *Erithacus rubecula*. *Anim. Behav.* 47, 679-686.

Sandberg, R. (2003). Stored fat and the migratory orientation of birds. In *Avian migration* (Eds. Berthold, P., Gwinner, E., Sonnenschein, E.; pp. 515-525). Springer, Berlin, Heidelberg.

Schmidt-Koenig, K. (1990). The sun compass. *Experientia* 46, 336-342.

Schmidt-Koenig, K., Ganzhorn, J. U., and Ranvaud, R. (1991). The sun compass. In *Orientation in birds*, pp. 1-15. Basel: Birkhäuser.

Senner, N. R., Conklin, J. R., and Piersma, T. (2015). An ontogenetic perspective on individual differences. *Proc. R. Soc. B* 282, 1-9.

Senner, N. R., Hochachka, W. M., Fox, J. W., and Afanasyev, V. (2014). An exception to the rule: carry-over effects do not accumulate in a long-distance migratory bird. *PLoS ONE* 9(2), e86588. doi:10.1371/journal.pone.0086588

Senner, N. R., Morbey, Y. E., and Sandercock. B. K. (2020). Editorial: The Degree of Flexibility in the Migration Strategies of Animals. *Frontiers in Ecol. Evol.*, in press.

Shamoun-Baranes, J., van Loon, E., Liechti, F., and Bouten, W. (2007). Analyzing the effect of wind on flight: pitfalls and solutions. *J. Exp. Biol.* 210, 82-90.

Shaw, P. (2017). Rainfall, leafing phenology and sunrise time as potential Zeitgeber for the bimodal, dry season laying pattern of an African rain forest tit (*Parus fasciiventer*). *J. Ornithol.* 158, 263-275.

Sergio, F., Tanferna, A., De Stephanis, R., Jiménez, L. L., Blas, J., Tavecchia, G., et al. (2014). Individual improvements and selective mortality shape lifelong migratory performance. *Nature* 515, 410.

Sjöberg, S., Alerstam, T., Åkesson, S., Schulz, A., Weidauer, A., Coppack, T., et al. (2015). Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea. *Anim. Behav.* 104, 59-68.

Sokolovskis, K., Bianco, G., Willemoes, M., Solovyeva, D., Bensch, S., and Åkesson, S. (2018). Ten grams and 13,000 km on the wing–route choice in willow warblers *Phylloscopus trochilus yakutensis* migrating from Far East Russia to East Africa. *Movem. Ecol.* 6, 20.

Stanley, C. Q., MacPherson, M., Fraser, K. C., McKinnon, E. A. and Stutchbury, B. J. M. (2012). Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. *PLoS One* 7,e40688.

Styrsky, J. D., Berthold, P., and Robinson, W. D. (2004). Endogenous control of migration and calendar effects in an intratropical migrant, the yellow–green vireo. *Anim. Behav.* 67, 1141–1149.

Sugasawa, S. and Higuchi, H. (2019) Seasonal contrasts in individual consistency of oriental honey buzzards' migration. *Biol. Lett.* 15, 20190131.

Sutherland, W. J. (1998). Evidence for flexibility and constraint in migration systems. *J. Avian Biol.* 29, 441-446.

Terrill, S. B., and Able, K. P. (1988) Bird migration terminology. *Auk* 105, 205-206.

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S. et al. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature* 535, 241-245.

Thorup, K., Alerstam, T., Hake, M., and Kjellén, N. (2003). Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proc. R. Soc. B.* 270 (suppl_1), S8-S11.

Thorup, K., Bisson, I. A., Bowlin, M. S., Holland, R. A., Wingfield, J. C., Ramenofsky, M., et al. (2007). Evidence for a navigational map stretching across the continental US in a migratory songbird. *Proc. Nat. Acad. Sci.* 104, 18115-18119.

Tickell, W. L. N. (1968). The biology of the great albatrosses, *Diomedea exulans* and *Diomedea epomophora*. *Ant. Res. Ser.* 12, 1–55.

Tryjanowski, P., Kuźniak, S., and Sparks, T. H. (2005). What affects the magnitude of change in first arrival dates of migrant birds? *J. Ornithol.* 146, 200-205.

Van Doren, B. and Horton, K.G. (2018). A continental system for forecasting bird migration. *Science* 361, 1115-8.

Van Doren, B. M., Horton, K. G., Dokter, A. M., Klinck, H., Elbin, S. B., and Farnsworth, A. (2017). High-intensity urban light installation dramatically alters nocturnal bird migration. *Proc. Nat. Acad. Sci.* 114, 11175-11180.

Van Doren, B., Liedvogel, M., and Helm, B. (2016). Programmed and flexible: long-term Zugunruhe data highlight the many axes of variation in avian migratory behaviour. *J. Avian Biol.* 48, 155-172.

Vardanis, Y., Klaassen, R. H., Strandberg, R., and Alerstam, T. (2011). Individuality in bird migration: routes and timing. *Biol. Lett.* 7, 502-505.

Vardanis, Y., Nilsson, J.-Å., Klaassen, R. H,. Strandberg, R., and Alerstam, T. (2016). Consistency in long-distance bird migration: contrasting patterns in time and space for two raptors. *Anim. Behav.* 113, 177-187.

Vega, M. L., Willemoes, M., Thomson, R. L., Tolvanen, J., Rutila, J., Samaš, P., et al. (2016). First-time migration in juvenile common cuckoos documented by satellite tracking. *PloS one* 11, e0168940.

Visser, M. E., Caro, S. P., van Oers, K., Schaper, S. V., and Helm, B. (2010). Phenology, seasonal timing and circannual rhythms: towards a unified framework. *Phil. Trans. R. Soc.* B 365, 3113-3127.

Watts, H. E., Cornelius, J. M., Fudickar, A. M., Pérez, J., and Ramenofsky, M. (2018). Understanding variation in migratory movements: A mechanistic approach. *Gen. Comp. Endocrinol.* 256, 112-122.

Watts, H. E., Robart, A. R., Chopra, J. K., Asinas, C. E., Hahn T. P., and Ramenofsky, M. (2016). Seasonal expression of migratory behavior in a facultative migrant, the pine siskin. *Behav. Ecol. Sociobiol.* 71, 9.

Weindler, P., Wiltschko, R., and Wiltschko, W. (1996). Magnetic information affects the stellar orientation of young bird migrants. *Nature* 383, 158-160.

Weimerskirch, H., and Wilson, R. P. (2000). Oceanic respite for wandering albatrosses. *Nature* 406, 955–956.

Weimerskirch, H., Åkesson, S., and Pinaud, D. (2006). Postnatal dispersal of wandering albatrosses *Diomedea exulans*: implications for the conservation of the species. J. Avian Biol. 37, 23-28.

Weimerskirch, H., Delord, K., Guitteaud, A., Phillips, R. A., and Pinet, P. (2015). Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. *Sci. Rep.* 5, 8853.

Wikelski, M., Arriero, E., Gagliardo, A., Holland, R. A., Huttunen, M. J., Juvaste, R., et al. (2015). True navigation in migrating gulls requires intact olfactory nerves. *Sci. Rep.* 5, 17061.

Willemoes, M., Strandberg, R., Klaassen, R. H., Tøttrup, A. P., Vardanis, Y., Howey P. W., et al. (2014). Narrow-front loop migration in a population of the common cuckoo *Cuculus canorus*, as revealed by satellite telemetry. *PLoS one* 9, e83515.

Willemoes, M., Blas, J., Wikelski, M., and Thorup, K. (2015). Flexible navigation response in common cuckoos *Cuculus canorus* displaced experimentally during migration. *Sci. Rep.* 5, 16402.

Wiltschko, W., and Wiltschko, R. (1972). Magnetic compass of European robins. *Science* 176, 62-64.

Wiltschko, W., and Wiltschko, R. (1992). Migratory orientation: magnetic compass orientation of garden warblers (*Sylvia borin*) after a simulated crossing of the magnetic equator. *Ethology* 91, 70-74.

Winkler, D. W., Gandoy, F. A., Areta, J. I., Iliff, M. J., Rakhimberdiev, E., Kardynal, K. J. et al. (2017). Long-Distance Range Expansion and Rapid Adjustment of Migration in a Newly Established Population of Barn Swallows Breeding in Argentina. *Curr. Biol.* 27, 1080-4.

Zehnder, S., Åkesson, S., Liechti, F., and Bruderer, B. 2002. Observations of free-flying nocturnal migrants at Falsterbo: occurrence of reverse flight directions in autumn. *Avian Sci.* 2, 103-113.

Figures

Figure 1. Geophysical basis of periodic migrations. A. Periodicities arising from planetary movements include annual cycles, diel cycles, and variants of lunar and tidal cycles; image: Edda Starck. **B.** Daylength (photoperiod) changes across the year at different latitudes. Daylength changes are locally predictably, but only for organisms that remain at the same latitude.

Figure 2. Synchronization of autumn activities. The graph shows data from captive young stonechats from different populations that hatched at different times of year under naturally changing photoperiods. Stonechats from all populations compensated for late hatching by earlier start of moult, faster moult, and younger ages at initiating Zugunruhe. Shown are on the y-axis the slopes of age at the onset and end of moult, and at the start of Zugunruhe, against hatch date on the x-axis (from left to right). Based on Helm et al. 2005. Inlay: stonechat during postjuvenile moult.

Figure 3. Responses to environmental factors depend on the phase of the annual cycle. Graphs show advance and delay responses of seasonal events (y-axis) to cues experienced at different times of year (x-axis). **A.** Alternating responses to temperature and precipitation, depending on the phase of the annual cycle, has been described as the dominant pattern of wild organisms based on 10,000 time series from the UK (Thackeray et al. 2016). Shown is the phase-dependent temperature response of egglaying in wild Barn Swallows (image kindly generated by Dario Massimino). **B.** Phase-dependent response of follicle growth to photoperiod in captive Garden Warblers (based on Gwinner 1996a). **C.** Schematic difference between migrants and residents in the phase-specific response to spring-like cues. In late winter and spring, long days and high temperatures advance subsequent life cycle stages, such as spring migration and reproductive activation. Conversely, later in the year the response reverses, and long days and high temperatures delay life-cycle stages. Long-distance migrants (inlay: Garden Warbler) differ from residents

(inlay: Great Tit) by a rigid phase during wintering, when long days and high temperatures have little or no effect on the annual cycle; image credit to commons.wikimedia.org: Garden Warbler by Kristjan Osbek, Great Tit by Biillyboy.

Figure 4. Mechanistic framework of spatio-temporal migration programs. Gray frame delineates the organism. It receives spatio-temporal information from the geophysical (yellow) and the biotic (green) environment, perceived through its sensory systems. This information is integrated with the animal's biological clock (blue) to generate internal clock time. Clock time modulates effector systems, which integrate additional modifying information (red) from within the body (e.g., fuel reserves) and from the environment (e.g., weather), to set the spatio-temporal migration behavior and physiology. Oscillator symbols indicate biological rhythms (central clock in inner circle, additional clock components peripheral). The clock system is itself modified by different factors (blue); for details see Helm et al. 2017.

Figure 5. Effects of food on Zugunruhe. Day-night activity shifts of a Garden Warbler in response to experimental changes in food supply. Shown is an actogram which plots activity of the bird (black marks) against time of day (x-axis) for each day of the experiment, represented by a line. Data are shown for two consecutive days: the second day is repeated as the first day on the successive line; actogram reproduced with kind permission of *Oecologia*. Inlay: image of Garden Warbler from Billyboy, Sweden, wikimedia.org; based on Gwinner et al. 1988.

Figure 6. Effects of geomagnetic cues on Zugunruhe. Actograms for first-year migratory Dunnocks monitored from 9 to 24 October 2015 under the local geomagnetic condition (control, top) and under simulated geomagnetic conditions (south displacements, bottom). Each horizontal line shows the mean time spent in flying mode by eight birds per group; days are duplicated for easier viewing as in Fig. 5 (except for first and last half-days). Dashed vertical lines indicate 12.00 hours local time (14.00 UTC), that is, the time when geomagnetic displacements took place

during the first 5 days of the experiment. Figure modified after Ilieva et al. (2018). Actogram reproduced with kind permission from *Animal Behaviour*.

Figure 7. Migration performance and route choices across time for migratory Black Kites tracked for 1-27 years. A. Migration routes of individually tracked Black Kites from breeding sites in southwestern Spain to wintering areas in West Africa. Pre-breeding tracks are shown in red and post-breeding tracks in yellow. **B.** Pre-breeding migration departure date in relation to Julian date advanced with age. **C.** Migration performance across and within individuals, illustrating that pre-breeding departure date improved rapidly during the first 7 years of life and then reached a plateau. In the initial years birds that survived within the next year (red) departed earlier (right axis) than those that died (blue). Similarly, within individuals, the repeatability of departure (black bars, left axis) was lowest in the initial years of life, when individual improvements (grey bars, left axis) were highest, and stabilized after birds were 7 years old. The cross-sectional pattern depicted in **B.** was concluded by Sergio et al. (2015) to be consistent with both within-individual improvements and selective removal of inferior performers. Figures from Sergio et al. (2014), reprinted by permission from *Springer, Nature*.

Figure 8. Carry-over effects across the annual cycle for migratory adult European Nightjars. A graphical presentation of distributions of stops and movements in the annual cycle for European Nightjars tracked by microdataloggers, plotted with respect to starting date 1 July. Black bars represent stationary periods and the pale gaps show time of movement. Grey sections refer to periods for which occurrence of stops could not be resolved. The dots show the individual's timing of the six distinct annual events as shown in inset, and the colour gradient shows the order of the birds in each event. Green illustrate the first bird and red the last bird, sorted by the date of arrival to the breeding area. From Norevik et al. 2018.

Figure 9. Examples of contrasting variation in migration routes. A. Common Cuckoo, B. Little Ringed Plover. A. Staging areas of eight satellite-tracked adult Common Cuckoos with vector directions between stopovers indicated by inserted orientation diagrams. Lines are connecting staging sites and do not necessarily represent the paths followed. From Willemoes et al. (2014). **B.** Autumn migration tracks of Little Ringed Plovers as revealed by geolocators. Filled small circles show three-day means of positional data and filled large circles are mean location for winter positions. Open circles indicate the location of a stopover period. Broken lines indicate unknown movement around the autumn equinox. Note that one individual was tracked for two consecutive migrations using different geolocators (male B). From Hedenström et al. (2014). Maps in Mercator projection.

Figure 10. Consistent, population-specific migration routes of Willow Warblers. A. Worldwide distribution of Willow Warblers. Breeding (yellow) and wintering (blue) ranges and occurrence during migration (hatched). Arrows (broken black) indicate the expected migratory routes of Scandinavian southwest-migrating *trochilus* and southeast-migrating *acredula* Willow Warblers, and their approximate initial wintering areas in sub-Saharan Africa. Black bar indicate location of hybrid zone between *acredula* (north) and *trochilus* (south) in Scandinavia. (Bensch et al. 2009; map courtesy Keith W. Larson, Sweden; Wikimedia.org). **B.** Migration of southwest-migrating *trochilus* Willow Warblers from breeding to wintering grounds (individuals represented by different colours; from Lerche-Jørgensen et al. 2017). **C.** Migration of *P. t. yakutensis* tracked by geolocation from breeding sites in Far East Russia to initial wintering areas in East Africa. From Sokolovskis et al. (2018).

Figure 11. Example tracks for adult Wandering Albatrosses recorded during sabbatical years representing the main movement strategies for birds breeding at Crozet and Kergulean Islands. Movement strategies are sedentary, sedentary with distant excursions of two Crozet birds, and migratory. The full cycle shows extremely long distance migration including two consecutive circumpolar movements of an adult from Kergulean Islands. After an initial rapid flight to Chilean waters where

the bird spent two months, it moved eastward through the Atlantic and the Indian Ocean (yellow) to reach the Chatham Rise, east of New Zealand, before returning to Kerguelen (orange) through the Pacific and Atlantic. Figures from Weimerskirch et al. (2015), reprinted by permission from Springer Nature/ /Palgrave.

Figure 1.JPEG

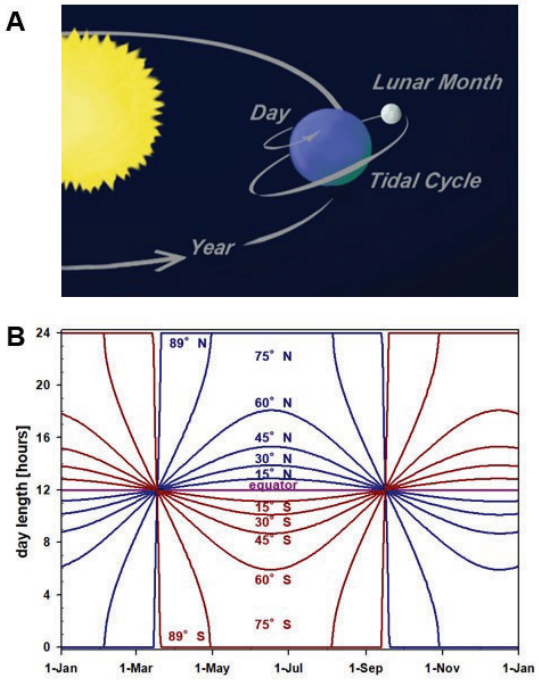


Figure 2.JPEG

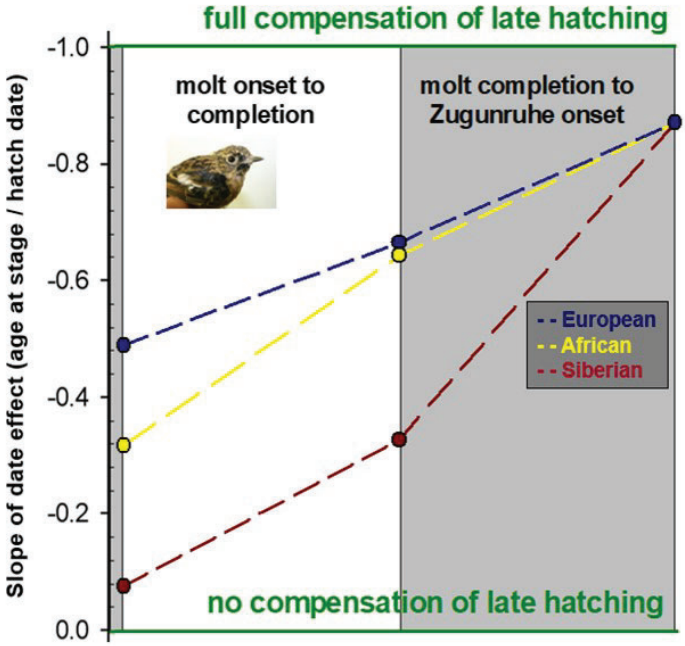


Figure 3.JPEG

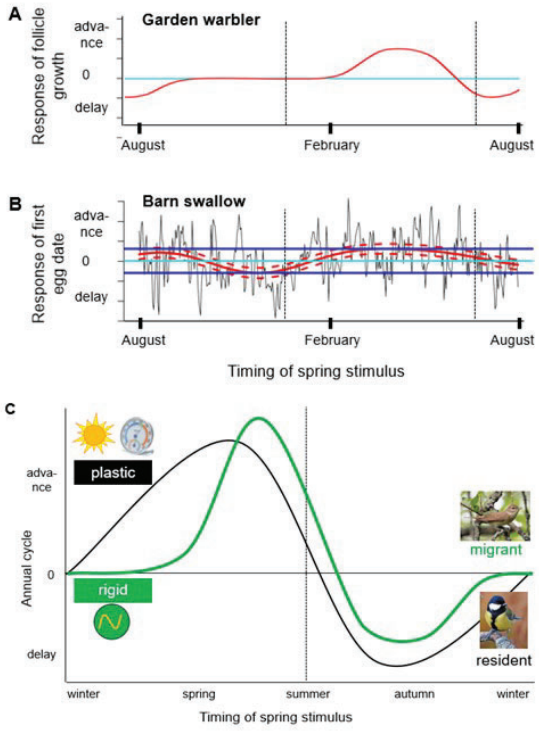


Figure 4.JPEG

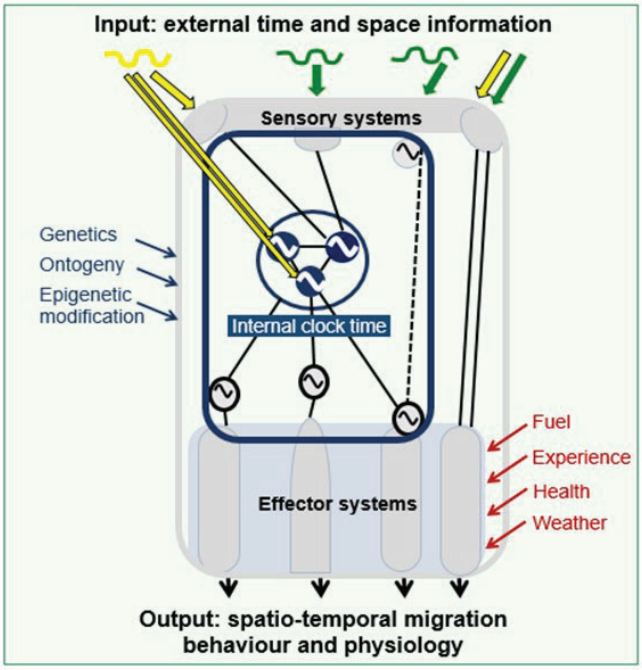
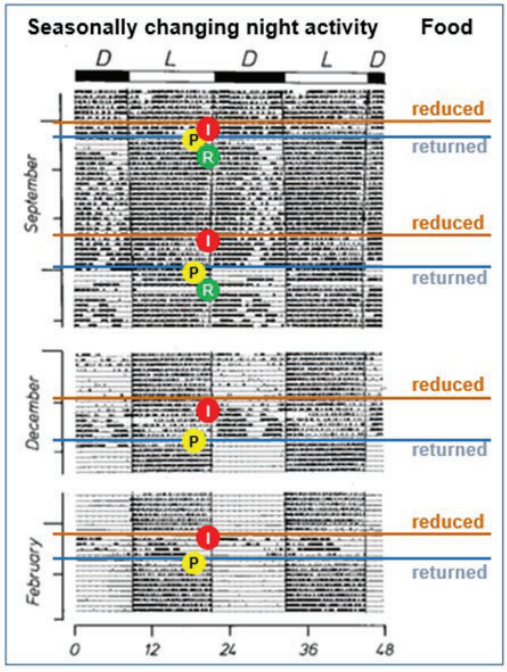


Figure 5.JPEG



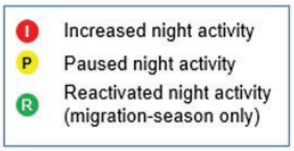


Figure 6.JPEG

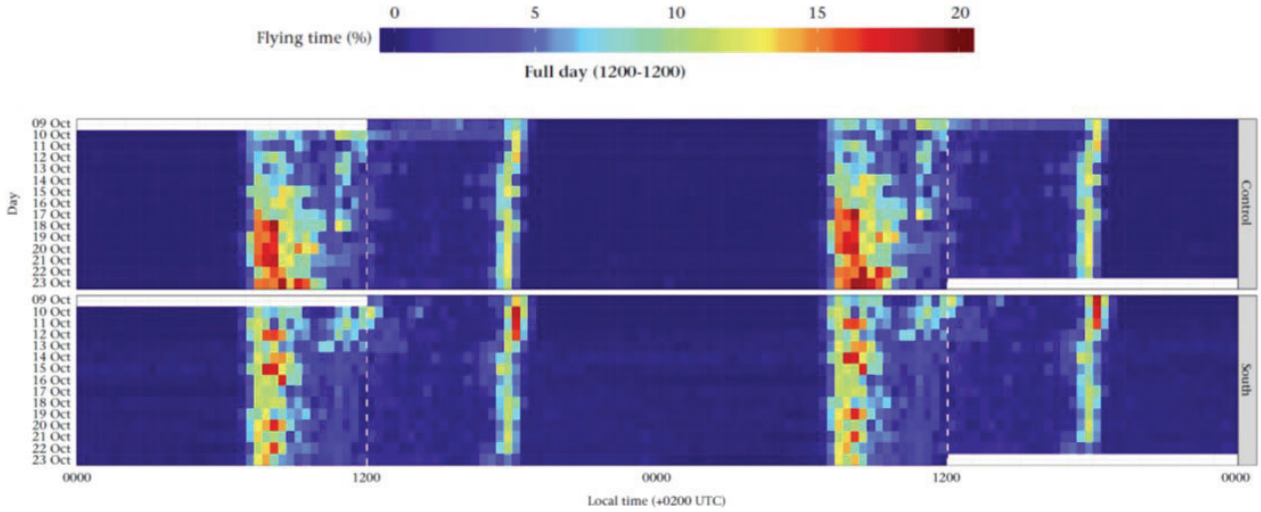


Figure 7.JPEG

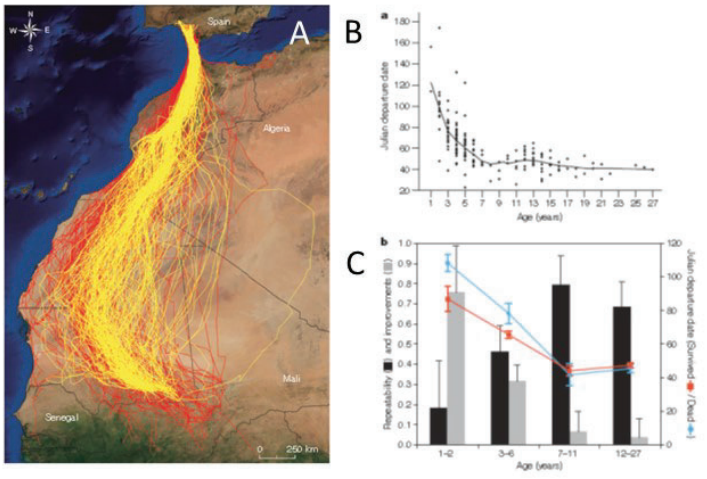


Figure 8.JPEG

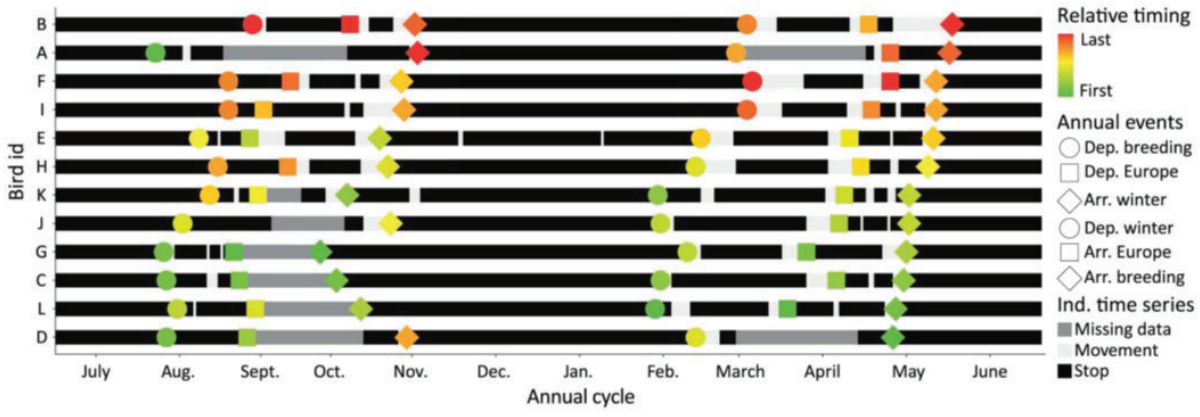


Figure 9.JPEG

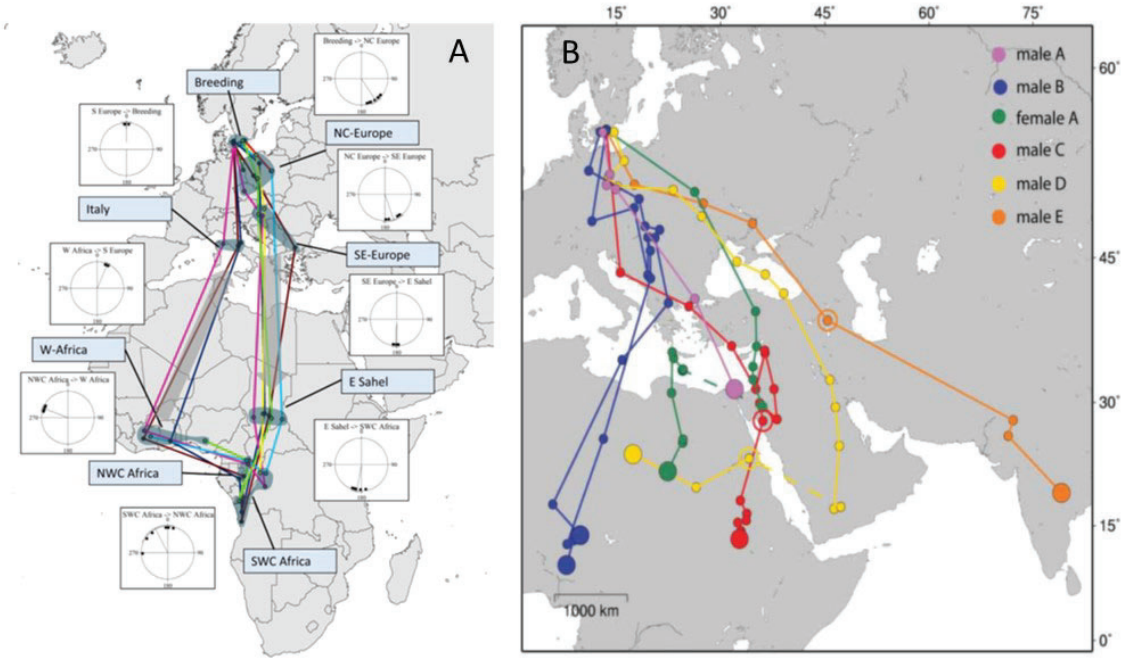


Figure 10.JPEG

Fig. 10

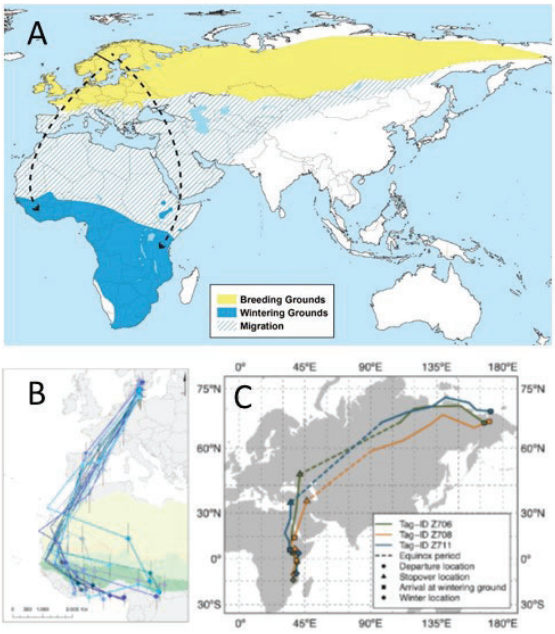


Figure 11.JPEG